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AN ANALYTICAL STUDY OF THE GEOGRAPHIC DISTRIBUTION OF RANA SEPTENTRIONALIS[1]

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Former investigations have disclosed a strong correlation between geographic distribution and certain adaptations of eastern American frogs. These adaptations concern embryonic temperature tolerance, rate of development, egg size, type of jelly mass, and temperature coefficient of development (Moore, 1949a). The general conclusions are as follows. If we compare northern and southern species of frogs we find that the former have a lower range of embryonic temperature tolerance, develop faster, have larger eggs, a more compact jelly mass, and a smaller temperature coefficient for development. Furthermore, in a given locality northern forms breed earlier than species with a more southern distribution. If the common eastern Ranas are arranged either in order of decreasingly extensive northern distribution or decreasing adaptation to low temperature the sequence is the same, namely, *sylvatica—pipiens—palustris—clamitans—catesbeiana.*

The species just listed are widely distributed. It is of interest to see if the generalizations for them can be applied to frogs having more restricted ranges such as *Rana septentrionalis* Baird (fig. 1). It is the purpose of this paper, therefore, to see what relation exists between embryonic adaptations and geographic distribution in *septentrionalis.* This species is confined to a relatively small area in northeastern North America. Its two closest relatives in this region are *Rana clamitans* Latreille and *Rana catesbeiana* Shaw. This last point is mentioned since throughout the paper comparisons will be made between *septentrionalis* and these related species.

Before we can evaluate the results on embryonic temperature adaptations it is necessary to compare the geographic distribution and breeding habits of *Rana septentrionalis* with those of the other species previously studied. When this is done we will be able to see where *septentrionalis* fits into the sequence of species given in the first paragraph.

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GEOGRAPHICAL DISTRIBUTION

Although *septentrionalis* is restricted to the northeastern part of North America it is not a "northern species" in the sense of being found in extremely cold areas. In fact its northern limit is probably not very different from that of *clamitans*.

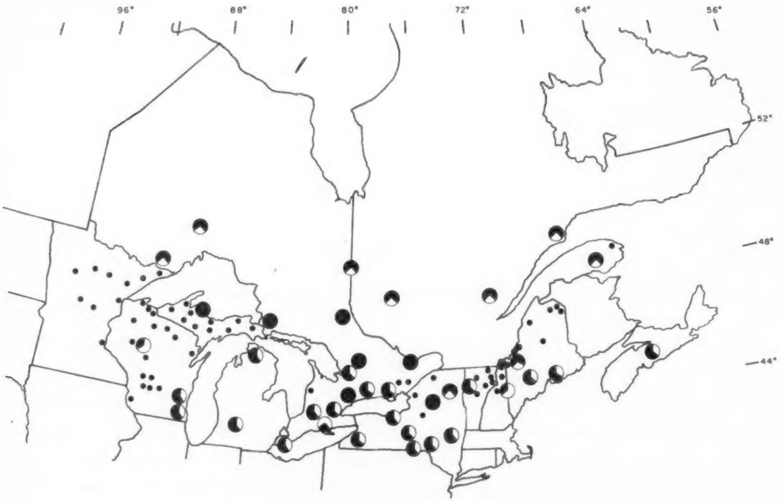

FIGURE 1. Geographic distribution of *Rana septentrionalis, Rana clamitans,* and *Rana catesbeiana.* The small dots represent records for *septentrionalis.* The circles are based on the locality lists discussed in the text. Parts of the circles are blackened if a species is present. If *septentrionalis* is present the upper right sector (0° to 120°) is black; if *clamitans* is present the upper left sector (240° to 360°) is black; if *catesbeiana* is present the lower sector (120° to 240°) is black.

The areas where *septentrionalis* is found are indicated in figure 1. This figure is intended to show two things, first the distribution of *septentrionalis* and second the presence or absence of *clamitans* and *catesbeiana* in the localities where *septentrionalis* is found. Small dots indicate isolated records for *septentrionalis.* The large circles are based on published local lists of amphibians. Different parts of the circles are blackened depending upon whether or not *clamitans, catesbeiana,* or *septentrionalis* are present. The following discussion will begin with the Gaspé Peninsula of Quebec and then move clockwise through the areas where *septentrionalis* is found.

The easternmost record for *septentrionalis* is Third Lake, a location twelve miles west of Gaspé Village (Ball, 1937). Moore and Moore (1939) found *septentrionalis* and *clamitans* but not *catesbeiana* at Cascapedia in the south-central part of the Gaspé Peninsula.

New records for New Brunswick and Nova Scotia are greatly to be desired. Mackay (1896) records *clamitans* and *catesbeiana* from Nova Scotia. Cox (1898) lists *catesbeiana* and *fontinalis* (= *clamitans*) as generally distributed in New Brunswick. No mention is made of *septentrionalis.* In his 1899a list of the amphibians of Gaspé and the Maritime Provinces he states that *septentrionalis* is found in Gaspé and New Brunswick but not on Prince Edward Island. When discussing *fontinalis* he writes, "Rather uncommon. Its place is taken by *R. septentrionalis* in Gaspé, New Brunswick and Prince Edward Island." In a paper appearing the same year (1899b) covering the same area he says of *septentrionalis* "abundant in all suitable places in Gaspé, where it takes the place largely of *R. fontinalis* Le Conte. Lately reported from New Brunswick. Not reported from Nova Scotia, nor does it occur in P. E. Island." In spite of these contradictions the last quotation is probably what Cox meant, but because of their indefinite nature it does not seem wise to accept these records. In view of the reports from Maine and Gaspé, however, we would expect *septentrionalis* to occur in northern New Brunswick.

All Maine records are north of the 45th parallel. In this area it is recorded by Pope (1915, 1918), Boulenger (1920), and Hoopes (1938). None of these give complete local lists, but Pope (1915) mentions that *catesbeiana* is found with *septentrionalis* at Ciss Stream, near Caucmogomac Lake, Piscataquis County. At Tim Pond, Eustis, Franklin County, Pope (1918) writes that, "*Rana clamitans* was found in the same situations, but was not nearly so abundant as *R. septentrionalis* while *R. catesbeiana* was conspicuous by its absence." Manville (1939) and Fowler (1942) have listed the amphibians of Mount Desert Island and Lake Cobbosseecontee, Kennebec County, respectively. In both areas *clamitans* and *catesbeiana* are present but *septentrionalis* was not observed.

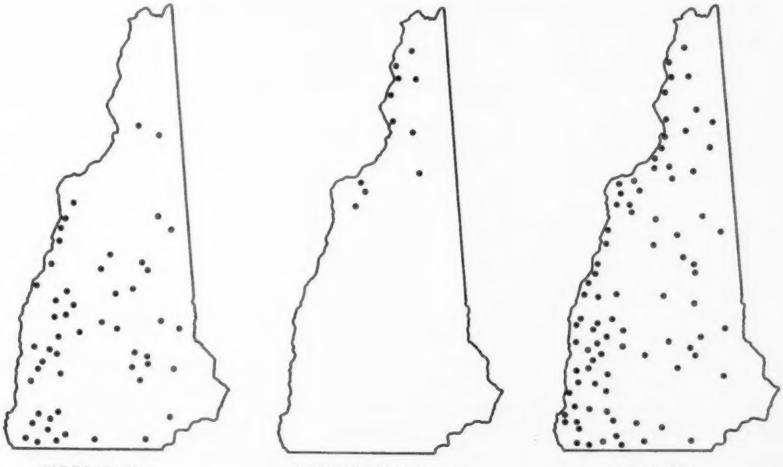

FIGURE 2. Geographic distribution of *Rana catesbeiana, Rana septentrionalis,* and *Rana clamitans* in New Hampshire. Based on Oliver and Bailey (1939).

New Hampshire records for *septentrionalis* are given by Oliver and Bailey (1939) and Aronson (1943). All of their localities are north of the 44th parallel. In figure 2 I have plotted their records for *catesbeiana, septentrionalis,* and *clamitans.* It will be noticed that *clamitans* is found wherever *septentrionalis* is found, but the latter and *catesbeiana* are together in only one locality.

Vermont records for *septentrionalis* are given by Hoopes (1938) and Trapido (1940). All localities are north of the 44th parallel. Hoopes remarks that all the New England *septentrionalis* localities known to her are above 1000 feet in elevation. Fowler and Cole (1938) list the amphibians of Stowe, Vermont. They found *clamitans* and *catesbeiana* but no *septentrionalis.*

Many records for *septentrionalis* have been given for northern New York by Cope (1889), Harper (1926), Weber (1928), Wright (1932), Wright and Wright (1949). Wright

(1932) mentions that 44° N. latitude represents the more common southern limit for this species in New York as well as in Ontario. He gives two definite records south of this parallel. One is at Onekio, Herkimer County, and in addition he reports that the United States National Museum has specimens of this species from Peterboro, Madison County. There is an old record of Mearns (1898) from the "Tamarack Swamp" near West Point. This locality may be the Tamarack Pond shown on the Schunemunk, N. Y., Quadrangle Map of 1935. The latitude of the latter locality is 41° 23′ and the elevation 1305 feet. This locality is far south of the other records for *septentrionalis* and I feel it should be regarded with doubt even though Mearns' specimens were identified by Stejneger. Dr. Doris M. Cochran advises me that these specimens are not in the collections of the U. S. National Museum. Neither are they at the American Museum of Natural History. If this record can be confirmed it will be the most southern locality for *septentrionalis.*

In a number of localities in central New York, *clamitans* and *catesbeiana* are found but not *septentrionalis.* These are Sullivan County (Evans, 1947), Albany County (Bishop, 1923), Alleghany State Park (Bishop, 1927), Tioga County (Clausen, 1947), Ithaca (Wright, 1914), Monroe and Wayne Counties (Wright and Moesal, 1919). I have found *septentrionalis* and *clamitans* but not *catesbeiana* in the lakes near Mount Marcy, Essex County. Wright and Wright (1949) mentions that all three species are found in Hellgate Ponds, Onekio, Herkimer County. This is the only New York report of these three species occurring together that is known to me.

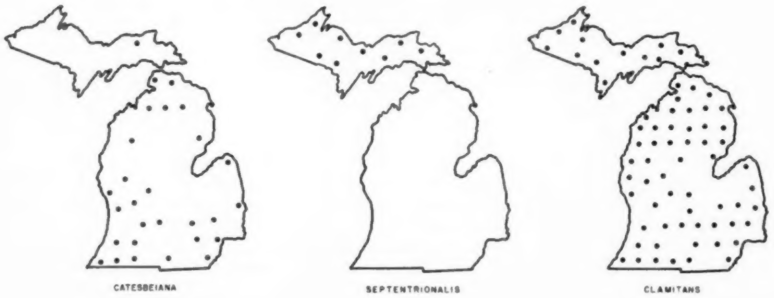

FIGURE 3. Geographic distribution of *Rana catesbeiana, Rana septentrionalis,* and *Rana clamitans* in Wisconsin. Based on Ruthven, Thompson, and Gaige (1928).

Rana septentrionalis has not been recorded from Pennsylvania or Ohio and the next (going west) United States records are from Michigan. The distribution of amphibians in this state is well shown by the records in Ruthven, Thompson, and Gaige (1928). Once again we note the interesting relation between the area occupied by *clamitans, catesbeiana,* and *septentrionalis* (figure 3). *Rana clamitans* is found throughout the state. With one exception all of the *catesbeiana* records are south of the area where *septentrionalis* occurs. Recently another locality in northern Michigan has been found where *clamitans, catesbeiana,* and *septentrionalis* are present, namely, in the Huron Mountains (Manville, 1948). Local lists for southern Michigan, where only *clamitans* and *catesbeiana* occur, are available for Kalamazoo County (Allen, 1937, 1938) and for the Douglas Lake region (Blanchard, 1928; Creaser, 1944).

The Wisconsin records are in sharp disagreement with the conclusions that can be drawn from nearly every other region. Pope and Dickinson (1928) report that *clamitans, catesbeiana,* and *septentrionalis* are statewide in their distribution. Local lists for Racine (Edgren, 1944) and Waukesha County (Cahn, 1929) report *clamitans* and *catesbeiana* but not *septentrionalis.* These latter two reports are for the extreme southeast corner of Wisconsin and should not be thought of as a contradiction of Pope and Dickinson. It is my feeling, however, that the distribution of *septentrionalis* in southern and central Wisconsin should be reinvestigated.

We are fortunate in having an excellent report from Minnesota (Breckenridge, 1944). His data for *catesbeiana, clamitans,* and *septentrionalis* are shown in figure 4. There is no overlap in the ranges of *catesbeiana* and *septentrionalis.*

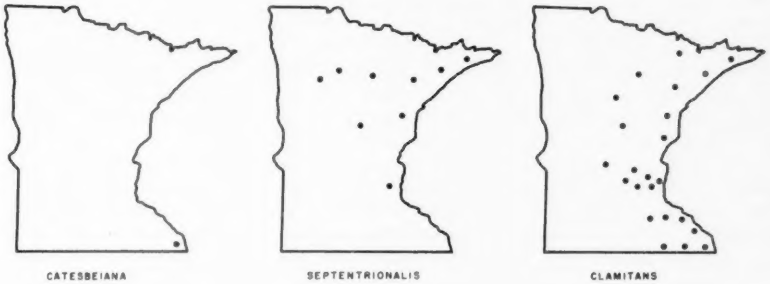

FIGURE 4. Geographic distribution of *Rana catesbeiana, Rana septentrionalis,* and *Rana clamitans* in Minnesota. Based on Breckenridge (1944).

Rana septentrionalis is not found west of Minnesota in the United States. It has been recorded as far west as Oregon and California by Yarrow (1883). His reports were based on material in the collections of the United States National Museum most of which, if we follow Cope (1889), was misidentified.

The westernmost record for *septentrionalis* in Canada is usually given as Selkirk Settlement in Manitoba. This is based on a statement by Seton (1918) which is, "Recorded by Kennicott as taken at Selkirk Settlement." I believe this refers to two specimens (catalogue number 5379) listed by Cope (1889) as collected by R. Kennicott at Selkirk Settlement. It should be noted that Cope does not indicate any province for Selkirk Settlement. In the case of all other specimens of *septentrionalis* he gives both the locality and the state or province. Dr. Doris M. Cochran has checked the U. S. National Museum records for me and her findings indicate clearly that the Selkirk Settlement record for *septentrionalis* should be disregarded. Specimen number 5376 is listed from "Selkirk Settlement" and the collector given as Donald Gurni (or Gwinn). The next three specimens listed in the catalogue were collected by R. Kennicott. The locality is indicated by ditto marks implying Selkirk Settlement. There is however, a question mark over the ditto marks. On this basis it would seem unwise to accept Selkirk Settlement as the locality for specimen 5379. It appears as though an error was made in cataloging.

Rana septentrionalis is widely distributed in Ontario. The most northern record is usually given as Hudson Bay or James Bay but unfortunately this too must be questioned. Cope (1889) lists under *Rana cantabrigensis evittata,* two specimens (catalogue number 5366) from "Moose River, B. America." It is generally accepted that this is the Moose River that enters the southern end of James Bay. Howe (1899) reexamined this material and concluded it was *septentrionalis.* Preable (1902) is of the same opinion but it is not clear whether he reexamined the specimens or merely accepted Howe's verdict. Williams (1920) saw one *septentrionalis* at Moose Factory (on the Moose River near James Bay). In view of the confusion surrounding Cope's specimens and the fact that Williams collected no specimens, I do not think it wise to accept these Moose River reports. In addition, Williams' sight record for Long Portage, Mattagami River (which I believe is at 49° 15′ N. and 82° 10′ W.), should not be accepted without specimens.

The most northern *septentrionalis* record that seems acceptable is Lake Nipigon (Logier, 1928). Here and at two other northern Ontario localities, namely, Quetico Provincial Park (Lindeborg, 1950) and Lake Abitibi (Dymond, 1928) *clamitans* and *septentrionalis* are recorded but *catesbeiana* is absent. In the area between 44° and 47° in Ontario there are many places where *clamitans, catesbeiana,* and *septentrionalis* occur in the same localities. These are Sault Ste. Marie (Logier, 1942), Temagami (Coventry, 1931), Dorset (Wright and Simpson, 1920), Ottowa (Patch, 1918), King Township (Logier, 1930; Ussher, 1939). The records of Toner and St. Remy (1941), for eastern Ontario, however, do not show much overlap of *catesbeiana* and *septentrionalis*. At the following localities in southern Ontario *septentrionalis* is absent, but *clamitans* and *catesbeiana* are found: Grippen Lake, Leeds County (Toner and Edwards, 1938); Hamilton (Brown, 1928); Point Pelee (Logier, 1925); Prince Edward County (Logier, 1941); Oxford County (Milnes, 1946); Darlington Township, Durham County (Allin, 1940). Additional Ontario records for *septentrionalis* will be found in Cope (1889) and Boulenger (1920).

Local lists are available for four localities north of the St. Lawrence River in Quebec. These are Lake Abitibi (Dymond, 1928), which lies on the Quebec-Ontario boundary, Wolf Lake, Northern Pontiac County (Grant, 1941), Laurentides Park (Vladykov, 1941), and Godbout (Trapido and Clausen, 1938). In every case *clamitans* and *septentrionalis* are found but *catesbeiana* is not reported.

With data so limited it is perhaps unwise to do more than speculate on the geographic distribution of *septentrionalis* and on the presence or absence within its range of the two closely related species, *clamitans* and *catesbeiana*. There are five localities between the 48th and 50th parallel in Quebec and Ontario for which we have good observations (refer to figure 1.) In every case both *clamitans* and *septentrionalis* are found together. While awaiting more data, the northern limit for both is set tentatively at Lake Nipigon, Ontario (50°N.). It is almost certain, however, that either or both are present in more northern localities. *Rana catesbeiana* is not recorded north of the Temagami District, Ontario (47°N.). Seton (1918) has a more northern record for *catesbeiana* in Manitoba but I find it unacceptable. The southern limit for *septentrionalis* is Peterboro, New York, and Crawford County, Wisconsin (this should be checked). Both are approximately 43° N. The area of possible overlap between *septentrionalis* and *catesbeiana* is, therefore, from 43°N. to 47°N. It should be clear, however, from the distribution data that have been presented that these two species are usually *not* found in the same locality. The only areas where there is any appreciable habitat overlap appear to be in southeastern Ontario and perhaps in Wisconsin.

BREEDING HABITS

The most complete life history study of *Rana septentrionalis* is that of Wright (1932). My own field acquaintance with this species is restricted to the Gaspé Peninsula of Quebec and the Adirondack Mountains of northern New York. In the latter locality the mink frog is common in the lakes of the Mount Marcy area. I have taken it at Heart Lake (altitude 2156 feet), Avalanche Lake (2863 feet), Lake Colden (2764 feet), and Marcy Dam (approximately 2250 feet). All of these localities are within ten miles of one another.

On July 12, 1940, egg masses were observed in Heart Lake. They were attached to the stalks of lily pads and were from 8 to 12 inches below the surface of the water. The jelly masses were globular and approximately 6 inches in diameter. The embryos were estimated to be in stage 19 (Pollister and Moore, 1937). They were light in color, in this respect reminding one of the larvae of *Rana palustris.* The temperature of the lake was 19° C. so it is probable that these eggs were deposited about July 7. A female collected at Heart Lake on July 3, 1941, had eggs in the uterus. Another collected at the same time had mature eggs in the ovary as did two collected June 15, 1950. From these observations I would tentatively conclude that breeding begins during the first part of July in this locality.

Rana clamitans eggs were seen in Lake Arnold on July 14, 1940 (water temperature 19° C.). From this observation and from an examination of the ovaries of females collected in this general area during June and July it would appear that *clamitans* and *septentrionalis* breed at more or less the same time.

In these Adirondack lakes one of the most striking things noticed about *septentrionalis* is its similarity to *clamitans.* The two species are found in the same type of habitat, apparently breed at the same time, and in coloration resemble one another closely. It is frequently difficult to distinguish between *clamitans* and *septentrionalis* of the same size. Mature individuals are easily separated since *clamitans* is a larger species.

Grant's (1941) observations in Pontiac County, Quebec, are similar. He notes that "*Rana clamitans* and *R. septentrionalis* thus occupy the same habitats and breed at the same time." He also noted the close morphological similarity between *clamitans* and *septentrionalis* and remarks that immature specimens of the former are almost indistinguishable from the latter.

Logier (1928) observed *clamitans* and *septentrionalis* in Lake Nipigon, Ontario. The *clamitans* of this area were dark in color, in this respect resembling *septentrionalis.*

Trapido (1940) has noticed the same phenomenon in northern Vermont: "...when we collect green frogs living in the 'black' water leached from the bogs surrounding northern glacial ponds, we find that they have become greenish black, and that the black dots are enlarged like the blotches of the mink frog. In coloration these might be mink frogs!"

Wright and Wright (1949) noted the parallel development of similar color patterns in *septentrionalis* and *clamitans* in northern New York. Other authors have drawn attention to the almost identical habits and external features of *clamitans* and *septentrionalis* but those quoted should be sufficient to show that this is a general phenomenon. The similarity of breeding time is important for the main thesis of this paper. The close resemblance of the two species in areas where the mink frog is found is of considerable interest. It will be treated in the discussion.

It should be clear from the data so far presented that it is not possible to fit *septentrionalis* exactly into the general scheme relating breeding habits, distribution, and embryonic adaptations that I have found for other eastern American frogs. Its breeding season approaches that of *clamitans* more closely than to that of any other species. The geographic distribution of the two, however, is different. The southern limit of *clamitans* is approximately 28° N. while that of *septentrionalis* is approximately 43° N. There is some uncertainty about the northern limits of the two but the best evidence seems to indicate they may be nearly alike in this respect. If we consider the breeding time and northern distribution alone, *septentrionalis* would fit into the sequence (see first paragraph of this paper) next to *clamitans.* If we used this place in the sequence as a basis for prediction, we might guess that *septentrionalis* would closely resemble *clamitans* in embryonic temperature tolerance, rate of development, and other adaptive embryological characters. If, on the other hand we emphasize the southern distribution of *septentrionalis,* we will come to a very different conclusion. The southern limit of this species is at the highest latitude of any eastern American *Rana,* being at 43° N. On this basis one would predict it to be a super-northern species, excelling even *Rana sylvatica* in adaptation to low temperature.

The data that will now be presented show that *septentrionalis* is a borderline species with respect to embryonic adaptations. In some ways it resembles northern forms (*sylvatica, pipiens,* and *palustris)* and in others it is like southern forms (*clamitans* and *catesbeiana*). Perhaps this compromise of northern and southern adaptations, with the result that it is not perfectly adapted for either type of environment, explains in part the restricted north-south distribution of this species.

TYPE OF JELLY MASS

The jelly mass of *septentrionalis,* which is well described by Wright (1932), is of the globular submerged type. In this respect it resembles *sylvatica, palustris,* and *pipiens* and differs from *clamitans* and *catesbeiana.* The two latter species have a surface film type of spawn. The jelly mass of *septentrionalis* is similar, therefore, to that of the cold adapted northern species (Moore, 1940).

Aronson (1943) observed spawning in one pair of mink frogs under laboratory conditions. He found the process similar to that of *pipiens.*

EGG SIZE

Measurements of four groups of uncleaved eggs gave these diameters in millimeters: 1.6 ± 0.0; 1.6 ± 0.0; 1.68 ± 0.03; 1.62 ± 0.01. A fifth group measured in the eight cell stage had a diameter of 1.68 ± 0.01. All of these eggs were from females collected in the Heart Lake region in the Adirondack Mountains of New York.

With respect to egg size, *septentrionalis* occupies an intermediate position between the early breeding northern group (*sylvatica, pipiens, palustris*) and the late breeding southern group (*clamitans, catesbeiana*). In the former the egg diameter is between 1.7 and 1.9 mm. In the latter group it is between 1.3 and 1.4 mm. (The data just quoted are for representatives of these species occurring in the New York area.)

EMBRYONIC TEMPERATURE TOLERANCE

The data on temperature tolerance and rate of development have been accumulated with the same methods that I have used in previous work. In all but one experiment eggs were obtained by pituitary injections and sperm by cutting up the testes in spring water. In one instance a female with eggs in the uterus was collected and brought back to the laboratory for prompt utilization. Mean values are given for the temperatures of the water in which the embryos were developing. Standard errors are given only if they exceed 0.1°. More complete details on methods will be found in Moore (1949b).

In the experiments that will be described the percentage of fertilization is usually lower than has been my experience with other amphibians. In the latter the per cent is usually 95 or above. In the case of *septentrionalis* it is frequently 50 per cent or less. The eggs that are fertilized, however, develop in a normal manner. In the one case where the female was gravid when collected, the per cent fertilization was about 95.

Pollister's frog stages (Pollister and Moore, 1937) are used to describe development. In some cases the letters "E," "M," or "L" follow the stage numbers and signify "early," "middle," or "late."

In an experiment begun July 18, 1950, embryos were raised at 33.6°, 32.0°, 30.4°, 27.5°, 24.6°, 19.9°, 15.5°, 12.9°, and 7.8°. The number of embryos available for each temperature was small so the temperature effects are evaluated on morphological grounds and not as the per cent developing normally. At 33.6° the embryos were badly injured by the high temperature and they died as abnormal blastulae. At 32.0° there was a definite temperature effect but the embryos fared somewhat better. There was a reduction in head size and severe circulatory system defects were observed. No embryo had gill circulation or heart beat at the morphological stages in which these were to be expected. The highest temperature at which any normal embryos were obtained was 30.4°. Even here there was some death in the neurula stage and slight defects in some of the embryos that developed beyond the neurula stage. There was no evidence of temperature injury at 27.5°, 24.6°, 19.9° or 15.5°. At 12.9° circulatory system defects were noticed. Heart beat was initiated but gill circulation never developed. The embryos were kept for 37 days and even at the end of this length of time gill circulation was not established. At 7.8° cleavage was prevented.

The data on rate of development are given in Table 1 and are plotted in figure 5. In the 27.5° experiment the embryos were at Stage 19L at 55 hours. They were next examined at 65.4 hours when they were found to be well formed stage 20. From their appearance at the two times I estimated that they probably entered stage 20 at 58 hours. At 24.6° I also failed to observe the embryos at the very beginning of stage 20. At 89.8 hours the embryos were already in this stage and from their degree of development it was estimated that the beginning of stage 20 was at 86 hours. It was necessary to suspend observations for a matter of days during the interval the 15.5° embryos would have reached stage 20. They were observed for more than 200 hours and from the data gathered it is possible to estimate with a high degree of accuracy the time they would have reached stage 20. The figure is 270 hours and it is arrived at in the following manner. At 19.9° stage 14 is reached in 36 per cent of the time required to reach stage 20. At 15.5° stage 14 (or 36 per cent of the time to stage 20) is reached in 97 hours. The total time to stage 20 can then be computed at 270 hours. Data are given for development at 12.9° even though only the early stages are

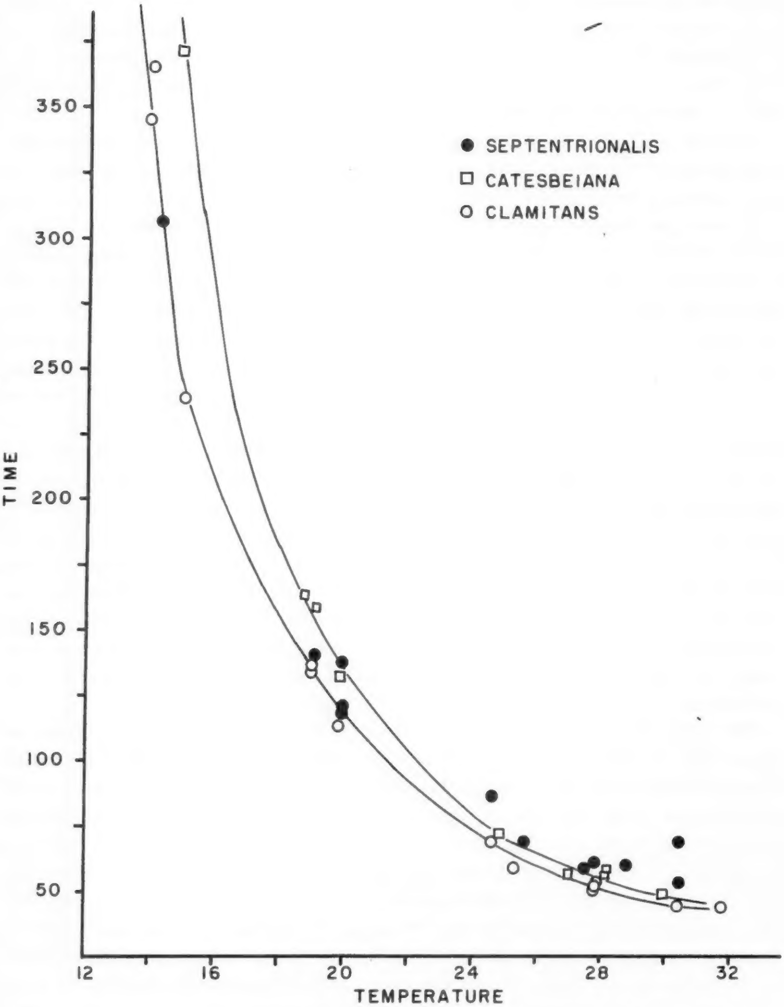

FIGURE 5. Rate of development of *Rana septentrionalis*, *Rana catesbeiana*, and *Rana clamitans*. The time required to reach gill circulation (stage 20) from first cleavage (stage 3) is plotted against centigrade temperatures.

TABLE 1

DEVELOPMENT OF RANA SEPTENTRIONALIS EMBRYOS AT DIFFERENT TEMPERATURES. EXPERIMENT OF JULY 18, 1950.

30.4°		27.5°		24.6°		19.9°		15.5°		12.9°	
Hours after Stage 3	Stage of development	Hours after Stage 3	Stage of development	Hours after Stage 3	Stage of development	Hours after Stage 3	Stage of development	Hours after Stage 3	Stage of development	Hours after Stage 3	Stage of development
0	3	0	3	0	3	0	3	0	3	0	3
5.5	8	5.7	8	5.3	8	5.7	7	17.2	8	17.2	7
17.0	12M-12L	17.0	12E	17.0	10M	17.0	9	30.1	9	30.3	8
20.0	13L	20.0	12M	20.0	12E	22.0	9L	41.3	10E	41.5	9
22.0	14E	24.0	14E	22.0	12	24.0	10	54.1	12E	73.0	9L
24.0	14M	25.6	14	24.0	13?	30.5	12E	66.0	12	78.3	10
30.0	16E	30.0	16E	30.0	14E	41.3	13	73.0	13E	90.0	11
41.3	17	41.2	17	41.3	16	47.0	13L	89.9	13L	95.0	12E
47.0	18	44.8	18	47.0	16	49.5	14E	97.0	14E	114.0	12M
54.0	18	47.0	18	54.0	17	53.8	14M	102.3	14M	138.0	13
65.6	19L	53.7	19L	65.5	18	65.5	16E	114.0	16E	150.0	13
68.6	20	55.0	19L	68.6	18	68.5	16	137.8	17	161.3	14E
		65.4	20	73.0	19	73.3	17E	161.3	17	188.3	14M
				89.8	20	90.0	17	188.3	18	199.0	15
						95.0	18	231.5	18	209.3	16
						102.3	18				
						114.4	19E				
						121.5	19				
						137.5	20E				

normal. None of the embryos at this temperature ever showed gill circulation, which is the criterion of stage 20.

On July 3, 1941, a female with eggs in the uterus was collected at Heart Lake near Lake Placid, New York. This female, together with males collected at the same time, was brought back to the laboratory and used the next day. At 31.4° some abnormal temperature effects were observed. As usual these appeared as injuries to the vegetal hemisphere during cleavage stages and defects in gastrulation. Stage 20 was reached in 53.5 hours after stage 3. At 30.4°, 27.8°, 25.5°, and 19.1° development was normal. The intervals, in hours, between stages 3 and 20 for these temperatures were 53.5, 61.5, 68.5 and 140. At 13.8° none of the embryos were completely normal. This must have been near the lower limiting temperature, judging from the extent of the temperature injury. Most developed as far as heart beat but none attained gill circulation. The rate data for this experiment are plotted in figure 5.

A third experiment, begun July 20, 1940, gave these results. No normal cleavage was observed at either 35.8° or 33.9°. At 32.3° the vegetal hemisphere was not divided into cells but in the animal hemisphere the cells reached the equivalent of a late blastula. None of the embryos gastrulated. At 31.5° the vegetal hemisphere was injured and no embryos developed entirely normally. Normal development was observed at 28.8°, 19.9°, and 14.2°. The intervals between stages 3 and 20 at these temperatures were 60, 120, and 304 hours. These data are used in figure 5. No normal development was observed at either 12.2° or 10.7°.

When all of the experiments are considered together the temperature range for normal development in *septentrionalis* can be fixed as 14°-31°. Temperatures of 7.8°, 10.7°, 12.2°, 12.9°, and 13.8° lead to abnormal development. Normal development occurs at 14.2 and 15.5. High temperature abnormalities sufficient to prevent fairly normal development have been observed at 31.4°, 31.5°, 32.0°, 32.3°, 33.6°, 33.9°, and 35.8°. Normal development takes place at 27.5°, 28.8° and 30.4° (two experiments).

In figure 5 a comparison is made of the rate of development of *septentrionalis, clamitans* and *catesbeiana.* The *septentrionalis* data are those reported in this paper plus one observation at 19.0° in which the interval between stages 3 and 20 was 119 hours. The data for *catesbeiana* are from my 1942 paper. The *clamitans* data are from my 1939 paper, together with subsequent observations.

The rate of development of these three species is similar. *Clamitans* develops faster than *catesbeiana* at all temperatures. At temperatures of 20° and below *septentrionalis* and *clamitans* are approximately the same. At temperatures above 24° *septentrionalis* is the same as *catesbeiana* or slightly slower. Observations at 19.8° are available for all three species. The interval between stages 3 and 20 is 112 hours for *clamitans,* 131 hours for *catesbeiana,* and in three experiments with *septentrionalis* 119, 120, and 137.5 hours. I am at a loss to explain this great variability in *septentrionalis.* I have not observed differences of this magnitude in individuals of other species (when the adults are from the same locality).

This emphasis on the minor differences in rate of development among *clamitans*, *catesbeiana*, and *septentrionalis* should not obscure the main point, namely, that in this character *septentrionalis* resembles *clamitans* and *catesbeiana* more closely than it does any other species.

The same general conclusion can be drawn from the data on temperature tolerance. As mentioned above the temperature range for normal development is 14-30° in *septentrionalis*. For *clamitans* the values are 12-32° and for *catesbeiana* 15-32°. The upper limit for *septentrionalis* is less than for the two related species and is identical with *palustris*. The lower limiting temperature for *septentrionalis* is intermediate between *clamitans* and *catesbeiana*.

DISCUSSION

The data presented in this paper are summarized in Table 2. With respect to breeding time, northern distribution, resistance of the embryos to low temperature, and rate of development, *septentrionalis* fits the general scheme of correlation between distribution, breeding habits, and embryonic adaptations shown by eastern American frogs. Its position in this scheme is that of a frog with the characteristics of the more southern species, *clamitans* and *catesbeiana*. With respect to egg size it is intermediate between the northern group (*sylvatica*, *pipiens* and *palustris*) and the southern group. In resistance to high temperature it appears to resemble *palustris* and thus occupies a somewhat intermediate position. The jelly mass of *septentrionalis* is of the northern type.

In respect to the southern limit of geographic distribution, *septentrionalis* is completely "out of line." The usual correlation between the geographical limit and embryonic adaptations breaks down completely in this one character. It is true that *septentrionalis* differs from *clamitans* and *catesbeiana* in having a northern type jelly mass and upper limiting temperature but it seems inconceivable that these could be the factor preventing *septentrionalis* from extending its distribution south of the latitude of central New York. After all *palustris* with the same upper limiting temperature tolerance as *septentrionalis*, and with a similar egg mass, extends almost to the Gulf of Mexico.

It is clear, therefore, that we must look to factors other than the embryonic adaptations studied for an explanation of the inability of *septentrionalis* to extend south of 43° N. I have one provisional hypothesis to suggest. In the section of geographic distribution, it was shown that in many localities *septentrionalis* and *catesbeiana* replace one another. The northern distribution of *catesbeiana* is consistent with its embryonic adaptations so it appears doubtful that *septentrionalis* is a factor in limiting the former's northern geographcial range. On the other hand, perhaps it is the presence of *catesbeiana* that prevents *septentrionalis* from extending its range further south. It should be noted in this connection that these two species occupy the same types of habit and might be expected to come into serious competition if sympatric. *Catesbeiana* is a huge frog, in fact the

TABLE 2

THE RELATION BETWEEN EMBRYONIC ADAPTATIONS, BREEDING TIME, AND GEOGRAPHIC DISTRIBUTION OF SOME EASTERN AMERICAN RANAS

Order of earliness in breeding	*sylvatica*	>	*pipiens*	>	*palustris*	>	*clamitans*	=	*septentrionalis*	>	*catesbeiana*
Northern limit	*sylvatica*	>	*pipiens*	>	*palustris*	>	*clamitans*	=	*septentrionalis*	>	*catesbeiana*
Resistance to low temperature	*sylvatica*	>	*pipiens*	>	*palustris*	>	*clamitans*	>	*septentrionalis*	>	*catesbeiana*
Rate of development at 20°	*sylvatica*	>	*pipiens*	>	*palustris*	>	*clamitans*	>	*septentrionalis*	>	*catesbeiana*
Egg size	*sylvatica*	>	*palustris*	>	*pipiens*	>	*septentrionalis*	>	*clamitans*	>	*catesbeiana*
Resistance to high temperature	*sylvatica*	<	*pipiens*	<	*palustris*	=	*septentrionalis*	<	*clamitans*	<	*catesbeiana*
Southern limit	*septentrionalis*	<	*sylvatica*	<	*palustris*	<	*clamitans*	<	*catesbeiana*	<	*pipiens*

Species with globular submerged jelly mass.	Species with a surface film egg mass.
sylvatica *pipiens* *palustris* *septentrionalis*	*clamitans* *catesbeiana*

largest in North America, and *septentrionalis* is one of the smallest. I know from personal observations that large *clamitans* will eat *septentrionalis* and *catesbeiana* would probably do the same. Perhaps this is a factor preventing *septentrionalis* from extending its range to lower elevations and to more southern localities. Field work in western New York and southeastern Ontario, where *catesbeiana* and *septentrionalis* have been reported from the same localities, should aid in the solution of the problem. The provisional hypothesis is, therefore, that competition with *catesbeiana* is one of the factors preventing *septentrionalis* from ranging farther to the south.

Another point, which was brought out in the section on breeding habits, concerns the striking similarity of *clamitans* to *septentrionalis* in regions where the latter occurs. The important point is that this similarity is most pronounced in those areas where the two species occur together. One possible explanation that suggests itself is that gene exchange between the two species is taking place. This would account for the continuous spectrum of pigment pattern connecting the "typical" *septentrionalis* and "typical" *clamitans*. The main difficulty with this suggestion is the inability of these two species to cross. *Clamitans* eggs cannot be fertilized with *septentrionalis* sperm, or in fact with the sperm of any foreign species. The eggs of *septentrionalis* can be fertilized with *clamitans* sperm but the hybrids develop only to the gastrula stage. In view of the current discussions of the possible role of introgressive hybridization in evolution, this similarity of *septentrionalis* and *clamitans* is of interest. It is just this sort of evidence that would lead one to conclude that introgression was taking place yet breeding experiments show clearly that this cannot be the explanation.

A second suggestion is that *clamitans* is mimicking *septentrionalis*. It is well known that the latter species gives off a notable and diagnostic odor when handled. Some find it resembling the odor of mink (hence the common name "mink frog") and others the odor of rotten onions. *Clamitans* does not have this aroma. Now if the scent of *septentrionalis* is of such a nature as to discourage its predators, *clamitans* could obtain some protection through mimicking the coloration of *septentrionalis*. There is no evidence, however, regarding the desirability, or lack of it, of the mink frog taste to its predators. A second difficulty with this hypothesis concerns the relative numbers of model and mimic. In the Adirondacks at least, *clamitans* appears to be the more abundant species.

A third suggestion, and the one that I feel is the most likely, is as follows. *Clamitans* and *septentrionalis* are found in the same habitat so it seems likely that natural selection would favor the evolution of similar pigment patterns. There are other cases of this in eastern American frogs. *Pipiens* and *palustris* are similar in pigment pattern and habitat. The same is true for *clamitans* and *catesbeiana* in areas outside of the zone where *septentrionalis* is found. In neither of these cases, however, is the resemblance between the two species so close as it is in *clamitans* and *septentrionalis*.

SUMMARY

Rana septentrionalis is restricted to an area bounded by Gaspé in the east, the 43rd parallel in the south, Minnesota in the west, and the 50th parallel (tentatively) in the north. It occurs with a closely related species, *Rana clamitans,* throughout this area. In general it replaces another closely related species, *Rana catesbeiana,* at higher elevations and in more northern habitats.

Data are given on temperature adaptations such as embryonic temperature tolerance, rate of development, egg size, and type of jelly mass. These data are considered in relation to geographic distribution and breeding habits of *Rana septentrionalis.* One would predict on the basis of the types of embryonic temperature adaptations shown by *Rana septentrionalis* that this species should range further south than it does. It is suggested that competition with *Rana catesbeiana* may be an important factor in restricting the southern distribution of *Rana septentrionalis.*

The striking similarity in coloration of *Rana septentrionalis* and *Rana clamitans* is thought to result from natural selection and not from gene exchange.

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ECOLOGICAL BARRIERS

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INTRODUCTION

One of the important and interesting problems in the biological sciences today is that of ecological barriers. These form one of the several different kinds of barriers or isolating mechanisms, to use Dobzhansky's (1937) now widely-accepted term, which have been described from time to time by students of various phases of evolution. For this symposium, ecological barriers should be of greater interest than the other types, but a brief sketch of the development of theories of isolation in general should not be amiss, especially since the distinctions between the different kinds of barriers are tenuous at best and since in many instances ecological barriers do not operate alone but in conjunction with isolating mechanisms of other types.

It is not easy to determine who was the first to appreciate the existence of natural barriers to hybridization. Probably the earliest suggestions of the importance of this factor in evolution were made about the middle of the Eighteenth Century; but it remained for Moritz Wagner to state the problem most clearly and effectively and to emphasize its importance as a major factor in evolution.

There appear to have been two periods during which isolating mechanisms have been most actively discussed and the many ramifications of the problem most avidly explored. The first period consists of the last half of the Nineteenth Century plus, perhaps, the first few years of the present. The second period includes chiefly the decade and a half which has just been completed.

The sterility of the intervening period was impressed upon the writer recently while looking through lecture notes from a course in evolution given in 1929 by the late Professor William Berryman Scott. In his comments on the work of Moritz Wagner, Professor Scott remarked, "Wagner got hold of an important principle, but it is usually overlooked now." The latter part of that statememt, true as it was twenty years ago, would be highly inappropriate today.

Wagner's emphasis was on separation in space and his concept of barriers was largely geographical. While he discussed ecological factors, especially climate, it was in connection with natural selection rather than as an additional type of barrier. Some of the other earlier biologists, however, realized that isolation was a principle of much broader scope and that anything that would prevent two related groups from producing fertile offspring together could be regarded as a type of isolation even though the two groups lived together in the same geographical region. The existence of different types of isolating mechanisms is well recognized today.

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Isolating mechanisms other than geographical were suggested by both Wagner (1873) and Jordan (1905) although they did not apply the term "isolation" to them, and apparently did not recognize them as such. Jordan maintained consistently that species are associated with physical barriers which both determine their range and are factors in their formation, and he even went so far as to hold that when the geographical origin of a species cannot be determined, it is because the species has not been studied critically. But in discussing *subspecies,* he apparently unconsciously suggested the possibility of ecological barriers. He believed that it was rare to find two subspecies inhabiting and breeding in exactly the same region, but when such appeared to be the case, he assumed the presence of a difference in habit or *habitat.*

Romanes (1886) saw that a very powerful isolating force arises if a variety shows some *sterility* with the parental form and the members of the variety are fully fertile among themselves. He based his argument in part on the fact that the reproductive system is the most variable part of the organism and he termed this type of barrier "Physiological Selection or Segregation of the Fit." This physiological isolation arises (Romanes, 1906) as a consequence of mutual infertility between members of any group of organisms and those of all other similarly isolated groups occupying simultaneously the same area.

ECOLOGICAL ISOLATION

Within recent years a number of different classifications of isolating mechanisms have been proposed by various authors. In general, they recognize a difference between purely extrinsic and purely intrinsic factors, as Dobzhansky (1937, 1942) and Hogben (1940) have emphasized, and they all have recognized and listed a number of different types of isolating mechanisms resulting solely or partially from intrinsic factors.

There is considerable confusion in the terminology of isolating mechanisms even if the earlier writings are omitted and only those since 1937 are considered. All classifications do not employ the same terms and some terms are used with different meanings by different writers. For example, Huxley (1940) includes the term "physiological isolation" but not "reproductive isolation" while Dobzhansky (1941) uses both terms and employs them interchangeably. Worthington (1940) includes both terms but does not use them synonymously and the same is true of Allee *et al.* (1949). Huxley (1940) uses "physiological isolation" to account for the physiological races of various parasites and phytophagous insects which may be very distinct even though they are morphologically very similar and Worthington (1940) points out that when used in this sense physiological isolation represents special cases of ecological isolation. On the other hand, Dobzhansky (1941), Mayr (1942), and Stebbins (1950) define "physiological isolation" to include all isolating mechanisms which are in part intrinsic, and therefore all mechanisms except the geographical. These isolating mechanisms are also referred to as "reproductive isolation" by these writers and also as "biological isolation" by Mayr. A third meaning of "physiological isolation" is that of Allee *et al.* who use it in a highly restricted sense when direct biochemical interaction prevents mating and results in a physiologic incompatibility between the sexes.

The term "reproductive isolation" similarly has had several meanings. Although Dobzhansky, Mayr, and Stebbins use it interchangeably with "physiological isolation" to mean all isolating mechanisms that are in whole or in part intrinsic, Allee *et al.* (1949) define it to include "any factor that prevents gene flow from one population to another such as spatial and ecological separation, as well as reproductive physiological or psychological incompatibility." They further elaborate on this by saying, "Even if the characters of the two populations are the same at the time of separation, and even if the environmental conditions are the same for the separated populations, they will gradually drift apart genetically through random changes in gene frequency, genetic fixation, and mutation." Worthington (1940) uses this term in a much more restricted sense to include "all barriers to breeding caused by reproductive behaviour in general, changes of generative organs, incompatibility of gametes, etc."

"Reproductive isolation," on the other hand, might be restricted to barriers that are in some way concerned directly with the reproductive structures or processes and with situations where the sexes fail to unite for reasons other than separation in space or time. Perhaps "generative" is preferable to "reproductive" in this sense since the latter has had a multiplicity of meanings.

With respect to their origins, the purely geographic and generative isolating mechanisms stand at the two extremes. Geographic barriers *per se* are purely environmental since they do not result from any reaction between the individual and his surroundings. It is a question, however, whether *purely* geographical barriers actually exist or whether, in many instances, barriers that are apparently geographic do not really separate two regions that differ ecologically.

Several isolating mechanisms seem to be determined by interaction both external and internal factors interacting. One of these, seasonal or temporal isolation, results from a difference in the time at which related groups come into their periods of reproduction. Numerous examples have been given in both plants and animals, but one of the more interesting is Hogben's (1940) reference to the moth, Eupithecia. Two species emerge at different times and therefore do not hybridize, but if the larvae of the earlier species are cooled the time at which they emerge is delayed, the barrier is removed, and hybrids can be produced.

With ecological isolation the extrinsic factor is concerned with space and this barrier therefore resembles geographical isolation. In fact geographic and ecological isolation are frequently not well delimited and many instances of apparently simple geographical isolation may prove upon more critical examination to result from small differences in the environment.

Stebbins (1950) has pointed out that the importance of purely geographic isolation may be greatly overemphasized, showing that members of the same species have upon occasion been completely separated geographically for millions of years without having differentiated into even subspecies, and that geographic races and allopatric species are usually separated by ecological barriers as well as by geographic ones.

Stebbins (1950) has distinguished between the ecological isolation of allopatric species and that of sympatric species. This is an important distinction in plants, but one that may not always be easy to apply. It is of little importance to the zoologist as sympatric species of animals are rarely separated by ecological isolating mechanisms.

Ecological factors act in several ways as barriers to hybridization. With some organisms they tend to keep the two parental types apart in space so that they simply do not hybridize in nature. Stebbins (1950) pointed out that one species of Platanus lives in the eastern part of North America and another in the Mediterranean region and that neither will grow spontaneously in the region of the other because of differences in climate adaptation. Vigorous, fertile hybrids can be produced artificially but would never arise in nature because the two species are too far apart spatially for gametic union.

In some genera, two species are restricted to different habitats but live within the same general area and presumably closely enough to hybridize. Frequently artificial hybrids are produced from them, indicating that no generative barriers are operating. The failure to find hybrids in nature from such species is sometimes attributed to an incompatibility between the developing hybrids and the habitat of either parent so that the hybrids do not find conditions under which they can proceed to develop to maturity, at least in competition with the parental forms, themselves. The effect is the same as with hybrid inviability or hybrid sterility except that if the barrier is generative the hybrid is inviable or sterile under all conditions whereas if it is ecological the hybrid will be inviable at least in competition in the habitats of the two parents but will grow to reproductive maturity in other habitats, presumably including zones intermediate between those of the two parental habitats.

With a view towards eliminating some of the confused terminology the following list of isolating mechanisms is suggested. It is admittedly eclectic and probably incomplete, but it is hoped that this classification includes some of the better features of the others.

I. *Generative isolation*—wholly intrinsic; includes "reproductive" and "genetic isolation" of Worthington.
  A. Reduction in mating.
    1. *Mechanical isolation*—differences in morphology of reproductive organs, specificity of insect pollinations, etc.
    2. *Gametophytic isolation*—incompatible pollen-tube growth.
    3. *Psychological isolation*—ethological factors involved.
  B. Failure of gametes to unite after mating.
    1. *Gamete-incompatibility isolation*—failure of sperm to enter egg.

        - 2. *Gene-cytoplasm isolation*—ejection or digestion of sperm after entering egg.
    - C. Failure of hybrids to reproduce after gametes unite.
        - 1. *Intrinsic hybrid-inviability isolation*—hybrids die before reaching sexual maturity for purely genetic reasons.
        - 2. *Hybrid-sterility isolation*—hybrids may grow vigorously but never produce viable and fertile gametes.
- II. *Non-generative isolation*—wholly or partly extrinsic.
    - A. Wholly extrinsic—*Geographical isolation*—includes both spatial and topographic isolation.
    - B. Dependent upon both intrinsic and extrinsic factors.
        - 1. Extrinsic factor is time—*Cyclic isolation*—includes both seasonal and temporal isolation.
        - 2. Extrinsic factor is space.
            - a. The parental species are allopatric—*Ecogeographic* isolation.
            - b. The parental species are sympatric—*Ecological isolation*; may operate largely by *ecological hybrid inviability.*

It must be remembered that most classifications are imperfect since they tend to reflect some approaches to the subject more strongly than others. Also, one should realize that classifications are rather the product of the human mind than necessarily something inherent in the subject. The very classification of isolating mechanisms tends to suggest that single barriers operate to separate species whereas frequently this is far from the case. In many genera it can be clearly shown that several barriers are acting together and it has been suggested that they frequently arise in a more or less definite sequence. This feature of isolating mechanisms must be recognized and needs much more study. This should be an interesting and fertile field for further observation, for it is quite likely that different combinations of barriers operate in different genera.

The suggestion has often been made that while geographic barriers may separate subspecies, only isolating mechanisms of an intrinsic nature can differentiate true species. Mayr (1942), for example, has stated that geographic isolation cannot alone lead to species formation because if two geographically isolated populations should meet they will interbreed freely unless a new set of barriers begins to operate. Dobzhansky (1937), too, has maintained that species are separated by the presence of intrinsic isolating mechanisms that prevent them from breeding together freely, whereas races and presumably other subspecific categories are not usually isolated in this way and, if at all, only very partially.

Geographical barriers, being purely extrinsic, can be broken down only by external changes. Barriers listed as solely intrinsic can be broken down, if at all, by biological changes such as artificial insemination, colchicine, or other treatment. Species isolated by seasonal or ecological mechanisms can often be crossed because of a change that eliminates either the extrinsic or the intrinsic barrier. The hereditary barrier might conceivably be eliminated by a gene mutation which would change the habitat preference. The temporal barrier has been occasionally eliminated by retarding development as in Eupithecia. The space factor separating ecologically isolated species can be eliminated by bringing the species together in the experimental garden or by creating an intermediate environment in the field. Whenever the barriers are eliminated, there is a possibility that hybrids can be produced and the presence of vast arrays of apparent hybrids in small regions of a general area has on several occasions led to a recognition of ecological barriers in the area.

Anderson and Hubricht's (1938) Tradescantia hybrids from the Ozarks and the Louisiana irises are two well-known examples of such ecological barriers. *Tradescantia canaliculata* and *T. subaspera* var. *typica* have been classed by taxonomists as good species. They are separated by a number of barriers in nature, the most important of which appears to be habitat preference, but they also differ somewhat in flowering season and, when they can cross, produce hybrids that are partly sterile. In spite of the last two partial barriers, they can hybridize and produce plants that can reproduce. Normally they are kept from crossing largely by ecological barriers, but can cross when the barriers are broken down in nature by erosion. Hybrids which closely resemble them can also be produced by artificial pollination in an experimental plot.

In southeastern Louisiana, *Iris hexagona* var. *giganticaerulea* and *I. fulva* are separated by ecological barriers (Riley, 1938, and Anderson, 1949), but when the barriers are broken, they also hybridize to produce a great host of intermediate types. Very little generative isolation is present, if any, and ecological preferences form the important mechanism. Ecological hybrid inviability is a very important feature of this barrier.

NATURAL HYBRIDIZATION

Since hybrid swarms are indicative of the break-down of ecological isolating mechanisms, it might be well to recall the great extent to which natural hybridization occurs in the plant kingdom. References to interspecific and even intergeneric hybrids are numerous in the floras and manuals of many regions, and it is obvious that only a very few of the many hybrid areas have been studied meticulously. Undoubtedly many different ecological factors operate as ecological isolating mechanisms and many different combinations of ecological and other barriers must separate species or incipient species in many genera. There should, therefore, be an abundance of material to engage the attention of ecologists, taxonomists, and phytogeographers for many years to come. While the fundamental problems are far better understood and appreciated now than they were a half-century ago, there are still many details to be investigated regarding the specific factors involved and their operation in many widely separated groups of plants.

Without attempting to include more than a small fraction of the published references to natural hybrids and hybrid swarms, it might be pointed out that many floras and manuals are replete with examples of hybridity in various groups of North American plants and that Anderson's excellent "Introgressive Hybridization" describes several of them in considerable detail and suggests techniques for studying them. A thorough review of natural hybridization has recently been published by Allen (1949).

Any attempt to obtain completeness in a list of natural hybrids must consider the fact that many undoubted hybrids are included in floras and manuals which are not actually listed as such by the author himself. For example, F. M. Bailey (1902) in "The Queensland Flora" described *Casuarina Cunninghamiana* as "A tree...closely resembling *C. equisetifolia* and *C. suberosa*...and possibly a variety of one or the other." Could this "species" not be a hybrid rather than a variety or is it to be considered a variety of one showing introgression of the other? Again, Bailey describes *Bulbophyllum intermedium* as having its name "suggested by its position intermediate between *B. Shepherdi* and *B. aurantiacum*." This plant, too, might well be a hybrid. A survey of similar references might supply an almost inexhaustible list of problems for the present-day naturalist. Are they hybrids? What barriers normally separate the parental species and what breaks them down? Studies on these last genera might well indicate some interesting differences in the nature of ecological barriers in Australia as contrasted with those of North America.

South Africa too seems to be a fertile field for a careful study of natural hybridization, for no sufficiently detailed and inclusive field studies have been made there although many putative hybrids have been listed by various authors. In the introduction to their three-volume work on the Stapelieae, White and Sloane (1937) state:

> Continued allowance should also be made by the collector for modifications of flower form in his specimens due to hybridization. This is particularly true in plants related to *Stapelia hirsuta* and *S. variegata*. Here the hybrids have become so numerous and so confused that any attempt to make one's specimens agree with the names on the labels that concurrently accompany them will probably be foredoomed to failure. Fortunately the number of true species is large.

White, Dyer, and Sloane (1941) mention hybrids in the succulent Euphorbieae, also, saying:

> The visit of two botanists from the Netherlands in 1926, Dr. J. P. Lotsy and Dr. W. A. Goddyn, who came to South Africa to study the hybridization of the native flora, helped to draw attention to the question of natural hybrids among the Euphorbias. In the course of their studies they bestowed names on two groups of plants which they believe to be definite hybrid crowds, *E. bothae* p.h. Lotsy & Goddyn. and *E. anticaffra* p. h. Lotsy & Goddyn.

These groups should now be given the kind of detailed study that was not generally conducted a quarter of a century ago. Another reference to a hybrid swarm has been made by Compton (undated) who has stated that two species of Cotyledon, the botterboom (*C. paniculata*) and the nentabos (*C. Wallichii*) occasionally grow side by side in the Hex River Pass and elsewhere. When they do, they apparently always hybridize, producing plants of the F_2 and subsequent generations. It would be very interesting to learn the types of barriers, probably ecological, that normally keep them apart.

Anyone who has made cytological studies of the Aloes and Gasterias knows the difficulties of making accurate determinations of the material. The chromosomes are beautiful for cytological studies, being large and relatively few, but the taxonomic difficulties are great. This taxonomic confusion was recognized many years ago by Berger (1908) and by Baker (1897). Berger listed and described a large number of naturally-occurring interspecific hybrids in Gasteria and Aloe as well as probable inter-generic hybrids between Gasteria and Haworthia, Aloe and Gasteria, and Lomatophyllum and Aloe. Baker included a statement after the description of several of the species of Gasteria or Aloe to the effect that the species was perhaps a hybrid or that it was a garden hybrid between certain species of the same genus, and he has also characterized some of the species listed as inter-generic hybrids. The need of a revision of the various genera of the Aloineae along modern lines is apparent from the numerous statements in the Flora Capensis that certain species were described from "a living plant in the Kew collection," or "the Vienna collection." Descriptions that seem to be even less reliable are those of *Gasteria repens* which is "described from a drawing of a plant grown at Kew in 1821" and of *Kniphofia Northiae* which is "described from a painting by Miss North and a living plant in the Cactus-house at Kew." Related genera have been treated equally lightly. For example, Smith (1948) pointed out that Resende published a description of *Haworthia lisbonensis,* a South African species, described from a plant found in the Botanical Gardens in Lisbon, Portugal.

The situation regarding the South African genera of the Aloineae appears to resemble the Louisiana irises in including numerous areas in which hybrid swarms occur. In an excellent discussion of the problem as it relates to the Haworthias, G. G. Smith (1948), a South African taxonomist, has indicated several such regions. For example, at Howiesons Poort, near Grahamstown, *H. Greenii* and *H. coarctata* grow side by side "surrounded by a mass of forms which include *Bakeri, minor* and *pseudo-coarctata.*" Smith suggests that a "splitter" could easily recognize a dozen or more forms. Other equally confusing areas have also been described.

The occurrence of so many probable hybrids in these genera indicates that generative isolating mechanisms are not fully operative and that, as in the Louisiana irises, ecological isolating mechanisms probably also play a part. Some unpublished observations of the writer upon some plants listed as species and received from the National Botanical Gardens in Kirstenbosch or the Huntington Botanical Gardens in California indicate that these putative species are almost completely pollen fertile while some hybrids apparently synthesized at the latter institution, are definitely somewhat more sterile. This relationship would indicate, if the designations of the species and hybrids are correct, that generative isolation was perhaps in an incipient stage but that it was not sufficiently well developed to be the only barrier.

The extent to which vegetative reproduction occurs must be taken into consideration in any study of speciation in this group, for almost all the species of Gasteria and many of those of the other genera put out suckers in abundance. For example, two putative hybrids between Gasteria and Aloe are completely pollen sterile (Riley, 1948) but put out so many suckers they can develop into large clones. Prolific vegetative reproduction reduces the importance of some types of generative isolating mechanisms, such as hybrid sterility.

Since generative isolating mechanisms alone do not prevent hybridization in the Aloineae, the probable existence of ecological barriers must be investigated by careful field studies. Smith (1948) is convinced that in Haworthia "opinions on systematics are likely to be of diminished value unless based partly on or correlated with the ecological aspect." Studies such as those of Clausen, Keck, and Hiesey (1940) would probably be necessary for a real understanding of these genera and it might be wisest in the long run to discard all species based (as many of them are) on single specimens grown under cultivation far from their natural surroundings. It might be mentioned that South Africa seems to be rather a fertile field for studies of hybridization in nature. Salter (1944), who has made extensive taxonomic studies, states that natural hybridization is common in many South African genera although, interestingly enough, his careful search in Oxalis has produced no satisfactory evidence for it in that genus.

It is evident that hybrid swarms exist in many genera of plants all over the world. The great innate variation to be found in the various groups of plants and the tremendous range of environmental conditions under which they live should produce almost limitless material for studies of speciation and isolation. In many genera definite progress will be made only by an investigator or group of investigators who combine the disciplines of taxonomy, ecology, and cytogenetics. Years ago, Kellogg (1908) stated that morphologists, cytologists, and laboratory men generally attached little importance to isolation and that only systematists, students of distribution, and so-called field naturalists recognized its importance. Fortunately, today, the academic isolating mechanisms have largely broken down and the laboratory and field men have intermingled for the betterment of biology.

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ARIDITY AS A STIMULUS TO PLANT EVOLUTION[1]

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The new combined attack on evolution from all directions: systematics, genetics, paleontology, ecology, and other fields, has brought into striking relief the great differences which have existed between the rates of evolution of different groups of organisms, or even within the same group at different periods of geological time. On the one hand, we have the types which have remained stagnant for millions of years: the *Ginkgos, Metasequoias, Cercidiphyllums,* and so on, and on the other hand the examples of very rapid, apparently "explosive" evolution; the tarweeds of California (tribe Madinae, family Compositae), the *Rubi, Hieracia* and *Crataegi* of the North Temperate zone, and the *Aegilops* species of the Mediterranean region. Evolution is not a series of even, steady trends, directed from within the evolutionary line, or from without by some preconceived plan or supernatural force. Rather it is opportunistic, depending upon the interaction between the hereditary variations which happen to exist in the evolving population at any one time, and the environment which happens to surround the population at that time. If we accept this premise, then we can legitimately ask the question: under what conditions of the environment can we expect maximum rates of evolution, and under what conditions will evolution become greatly retarded or even completely stagnant?

Simpson (1944) has given a partial answer to this question. He has pointed out that the static populations have nearly all existed in environments which have remained relatively constant and continuously favorable. For land plants, these are chiefly the great forest belts. Extending this reasoning, we might conclude that the most rapid evolution would occur in habitats which are changing, and in particular those which are limiting or deficient in some factor essential to the existence of the organism. In the present paper evidence is presented in favor of the hypothesis that environments limiting or deficient in one all important factor, moisture, have often promoted rapid evolution.

The hypothesis that evolution is more rapid in semiarid regions than in climates with continuously adequate moisture would seem to be contradicted by the fact that mesophytic communities are much richer in species than are xeric ones; and that the data available indicate that this richness holds true also for genetic variability within a species. Dobzhansky (1950) has recently produced evidence which strongly supports both of these generalizations in respect to the tropical rain forest. The fact must be remembered, however, that this comparative richness of mesic and poverty of xeric communities is based on observations made at only one level of geological time—the present. Evolution involves not only the origin of species, but also their migration and extinction. Even though a particular xeric community does not support many species at the present or at any one particular time, dry habitats may have supported as many or more species than the mesic ones over the whole scale of geological time because of a more rapid turnover in the species composition. In the drier areas, it is possible that more species originate, reach their climax, decline, and become extinct than in the more favorable regions. On the other hand, the present day richness of the more mesic communities may be due to the fact that they have accumulated species over a relatively long period of time. If their species are slow to die out, they may contain very old and much younger species side by side.

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[1] Read at a Symposium on "The Ecological Background of Evolution" before Section G of the A.A.A.S. and the Ecological Society of America at Cleveland, Ohio, December 29, 1950.

From the theoretical point of view, there are three reasons why we would expect evolution to be relatively rapid in arid or semiarid regions. In the first place, where moisture is a limiting factor, local diversity in topography, soil, and other factors will have a much greater effect on the character of the vegetation than in regions where moisture is adequate. This can be easily seen when one compares the flora of the Coast Ranges of California with that of an area in the eastern United States, such as the White Mountains, Adirondacks or Alleghenies, which is comparable in latitude, topography, and soil types. The California flora as a whole is as rich or richer in species than the eastern ones, but the individual communities are much poorer. The richness of the California flora is due to the existence in the same restricted area of many different communities, so that the concept of a single climax association determined by the climate is difficult or impossible to apply. In the Santa Lucia Mountains, for instance, one can walk along a north-facing slope through a lush redwood forest, carpeted with ferns, broad-leaved Aralias, and other extreme mesophytes, and, looking across at the south-facing slope on the other side of the canyon, see a sparse association of yuccas, sclerophyllous shrubs, xerophytic bunch grasses, and small annuals. In other parts of the same canyon or mountainside, a whole series of intermediate types of associations can be found. This diversity of habitats promotes a corresponding geographic differentiation of the species and genera inhabiting these areas. Clausen, Keck, and Hiesey (1940) were the first to demonstrate the richness in ecotypes of certain California species; this regional genetic diversity is probably true of a large proportion of the species of coastal California. Furthermore, many of the conspicuous California genera, such as Ceanothus, Arctostaphylos, Diplacus, Lupinus, and Calochortus, form a mosaic of allopatric or ecologically differentiated species or strongly marked subspecies. In the large genera of the eastern states, the species of a genus are much more likely to be sympatric, and one might predict that the diversity in ecotypes of individual species, when investigated, will prove to be considerably less.

This regional diversity of species and genera in arid or semiarid regions has two important effects on evolution. In the first place, the frequent geographic or spatial isolation provides many situations favorable to the origin of other reproductive isolating mechanisms, and hence to speciation. Secondly, climatic fluctuations will cause frequent merging of previously isolated and differentiated races or species, and hence give many opportunities for the increase of genetic diversity through hybridization and introgression, as suggested by Anderson (1949).

The second reason why semiarid climates, with their regional diversity, may be expected to promote rapid evolution, is that the population structure of the component species is likely to be particularly favorable. Wright (1940) has pointed out that the most favorable structure for rapid evolution is that of a large or medium sized population divided into many small subunits or colonies which are largely isolated from each other, but can interchange genes through occasional migration between colonies. Such a population structure permits new gene combinations to become established in the individual subunits, both through natural selection and chance fixation, without the swamping effect which occurs in large populations. At the same time, migration between colonies prevents their stagnation, and allows the population as a whole to draw upon a large supply of genes. In arid or semiarid regions, with their regional diversity, this type of population structure may be expected much more frequently than in areas with abundant moisture.

The third reason for rapid evolution in arid or semiarid regions is the number of different specialized structures which plants can evolve for adaptation to dry conditions. Reduction in leaf surface, development of trichomes, scales and other coverings, of sunken stomata, of deciduous leaves, of extensive root systems, of bulbs, storage roots, and other structures which aid in dormancy, of a special physico-chemical nature of the protoplasm; all of these appear as frequent modifications of xerophytes. Furthermore, most xerophytic associations, particularly in warmer regions, contain species with a variety of different modifications or combinations of them, so that these associations are remarkable for their diversity rather than their uniformity. Their species, though relatively few in number, present a variety of different life forms.

Although no good data are available on this point, we might expect that even within some of the species, different races would differ in their adaptations to xerophytism. A race might differ from its neighbor in possessing a more poorly developed root system, but compensate for this deficiency through a more strongly developed indumentum, a greater ability to go dormant, or more efficiently constructed protoplasm. Such adaptational diversity within a species would be particularly favorable for further divergent evolution.

In semiarid regions, divergent evolution will not necessarily be confined to adaptations toward xerophytism. If the climate of such a region is becoming progressively more moist, we can expect that some of the xero-

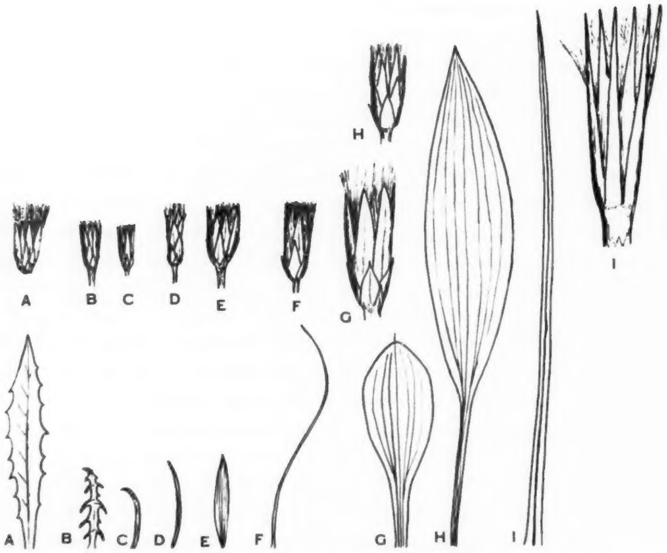

FIGURE 1. Foliage leaves (× ⅓) and involucres (× ⅔) of various species of the genera Stephanomeria, Scorzonera, and Tragopogon. Drawn from specimens in the herbarium of the University of California.

A. *Stephanomeria cichoriacea* Gray, involucre from San Antonio Canyon, Calif., Mrs. C. M. Wilder 589; leaf from Hepsedam Peak, San Benito County Calif., H. M. Hall 9932.

B. *S. Parryi* Gray, from Panamint Range, Inyo County Calif., E. Crum 2061.

C. *S. pauciflora* (Torr.) Nelson, from Grand Junction, Colo. S. G. Stokes in 1900.

D. *Scorzonera divaricata* Turcz., from Shabarakh Usu, Outer Mongolia, R. W. Chaney 68.

E. *S. cinerea* Boiss., from Bulgar Dagh Turkey, Eig and Zohary in 1931.

F. *S. purpurea* L., from Transsilvania, Pancic, s. n., U.C. no. 32047.

G. *S. Auberti* Br.-Blanquet et Maire, from near Fez, Morocco, Wilzek in 1933.

H. *S. humilis* L., from Södermanland, Sweden, E. Asplund in 1929.

I. *Tragopogon porrifolius* L., from living plant collected in Berkeley, Calif.

phytes with favorable population structure will become readapted to moist conditions. Furthermore, the ways in which this readaptation can be accomplished are very numerous. Hence related xerophytes, becoming readapted to moist conditions under the influence of the same climatic change but in regions isolated from each other, could continue their divergent evolution. In this way, the flora of the same mesophytic region could come to contain members of the same family or tribe, all adapted to essentially similar conditions, but adapted in different ways and hence very different from each other because of their different evolutionary histories.

The writer first saw evidence of this type of evolution in his studies of the tribe Cichorieae of the family Compositae. Two closely related genera of this tribe, Scorzonera and Tragopogon, though confined to the Old World, are not clearly related to any other Old World genera, but some of their species show a marked resemblance to the New World genera Stephanomeria, Lygodesmia, and Chaetadelpha.

The most distinctive species of Scorzonera and Tragopogon have leaves which are either linear and grass-like or elliptic, parallel-veined, and entire-margined, in any case very different from the lanceolate and dentate or pinnatifid leaves characteristic of most species of the tribe (figure 1, G, H, I). Furthermore, they have very large involucres and achenes. This enlargement is probably secondary, since the achenes do not possess the complex vascular anatomy found in primitive large-headed Cichorieae, such as the species of Dubyaea (Stebbins, 1940). Furthermore, the largest involucres and achenes are found in species of Tragopogon, which is highly specialized as to both involucres and achenes.

These most specialized species of Scorzonera and Tragopogon are mesophytes, living in fields and meadows in company with species of Hypochaeris, Leontodon, and other typical genera of the tribe Cichorieae. The more generalized species of Scorzonera, on the other hand, are xerophytes of the central Asiatic steppes. This whole situation is best explained by postulating the following course of evolution. The original ancestor of Scorzonera was a mesophyte or semi-xerophyte, with elliptic, dentate or pinnatifid leaves similar to those of the modern *Stephanomeria cichoriacea* (figure 1A). From

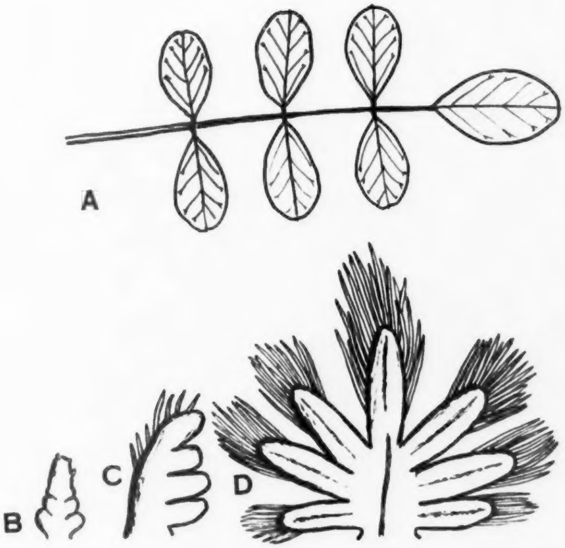

FIGURE 2. Mature leaf (A) and three developmental stages (B, C, D) of *Colutea arborescens* L., from material collected on the campus of the University of California, Davis. A, × ⅓; B-D × 33.

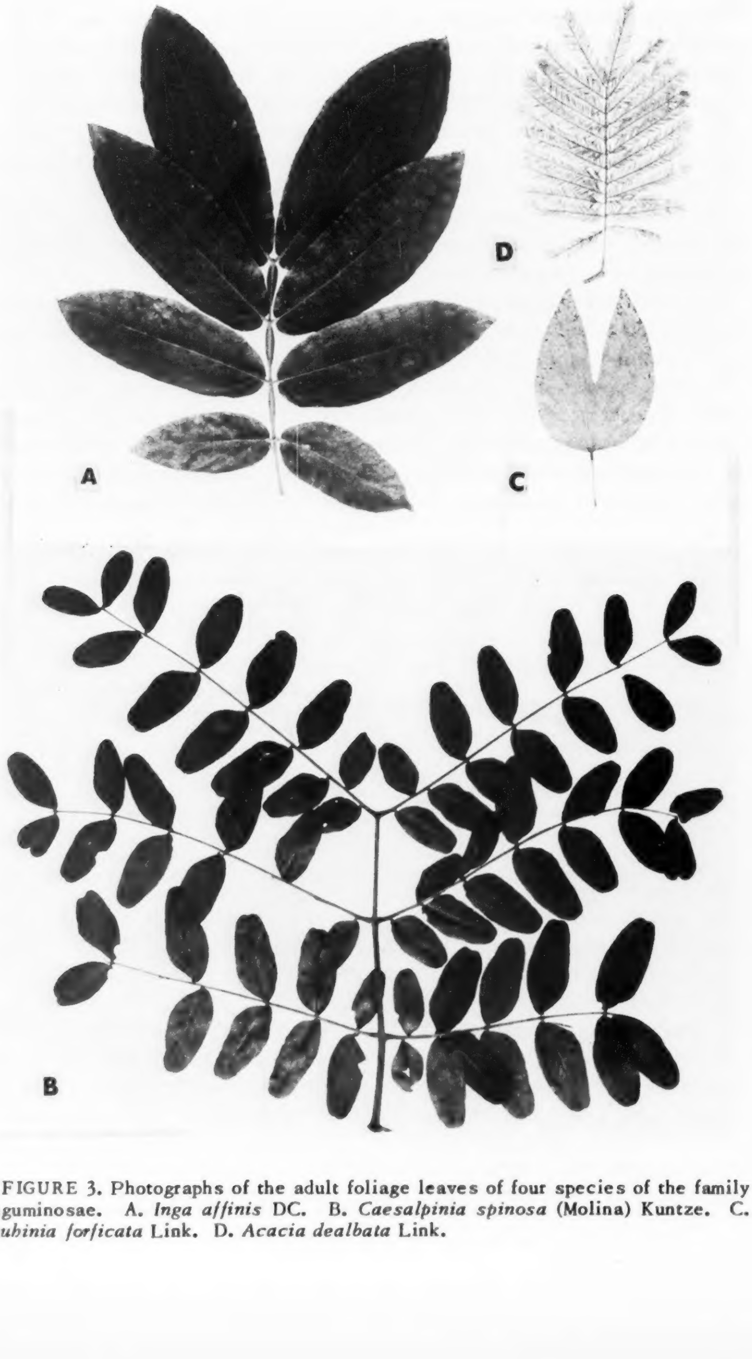

FIGURE 3. Photographs of the adult foliage leaves of four species of the family Leguminosae. A. *Inga affinis* DC. B. *Caesalpinia spinosa* (Molina) Kuntze. C. *Bauhinia forficata* Link. D. *Acacia dealbata* Link.

this type there evolved xerophytes with reduced leaves, either pinnatifid like those of *Stephanomeria Parryi* (figure 1B), or entire like those of most specimens of *Stephanomeria pauciflora* (figure 1C). This is the condition in the xerophytic *Scorzonera divaricata* (figure 1D) of central Asia, one of the most primitive species of its genus. From a type such as this, the more advanced, mesophytic species of Scorzonera and Tragopogon evolved through elongation and in some instances broadening of the leaves, reduction in the amount of branching of the plant, and increase in size of the involucres and achenes.

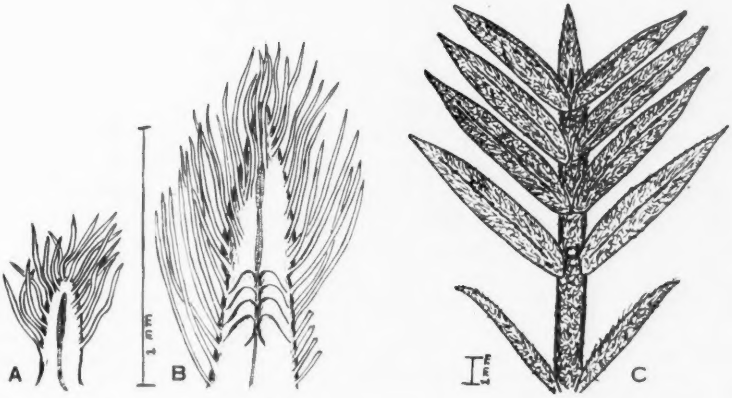

FIGURE 4. Stages in the development of the foliage leaf from an old tree of *Inga affinis*, material collected in Franceschi Park, Santa Barbara, Calif. A and B, × 33; C × 3.3.

Another series of examples of reversal toward mesophytism is found in the leaf types of the family Leguminosae. Two of the most common leaf types found in this family are the odd-pinnate leaf and the even-pinnate leaf. The former, which is most common in the subfamily Papilionoideae, possesses several pairs of lateral leaflets and a conspicuous terminal leaflet (figure 2A). The even-pinnate type of leaf, on the other hand, possesses only lateral leaflets, the terminal one being replaced by a tiny, vestigial rudiment, which usually drops off as the leaf matures (figure 3A). This type is found most commonly in the subfamily Caesalpinoideae, but occurs also in the Mimosoideae and occasionally in the Papilionoideae. Superficially, the difference between the two types seems to be merely the presence or absence of the terminal leaflet.

Studies of developing primordia, however, have shown that the course of development in two species with even-pinnate leaves, *Ceratonia siliqua* L. of the subfamily Caesalpinoideae and *Inga affinis* D.C. of the subfamily Mimosoideae, is entirely different from that in odd-pinnate leaves, of which *Astragalus Cicer* L. (Troll, 1939) and *Colutea arborescens* L. may be taken

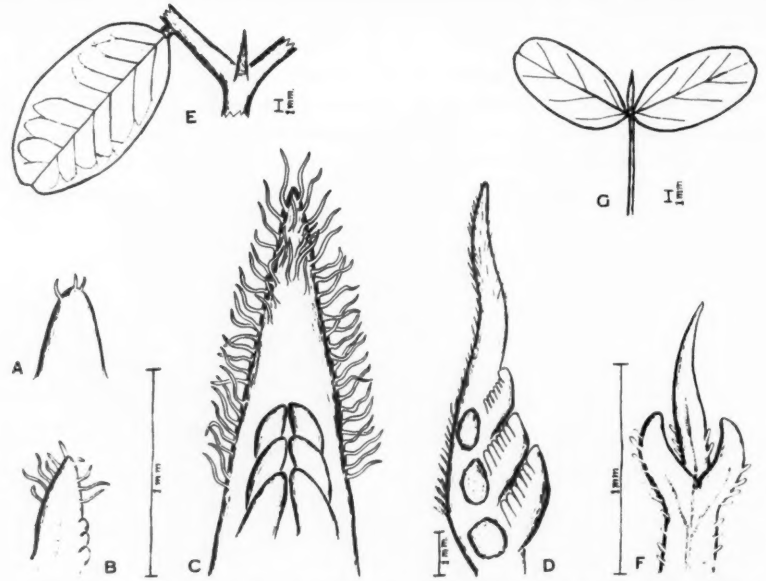

FIGURE 5. A-D, stages in the development of a leaf on a mature shoot of *Caesalpinia spinosa.* E. End of the leaf rachis and a single leaflet of a mature leaf, to show the vestigial point of the rachis. F and G. Young and mature stages of the second leaf formed on the seedling of *Caesalpinia spinosa.* All material collected from a street tree and its seedlings on Garden Street, Santa Barbara, Calif. A-C and F, × 33, D × 6.7, E and G × 1.7.

as typical. In the odd-pinnate leaf of Colutea (figure 2), the terminal leaflet is developed slightly before the lateral ones, but this difference is not great, and by the time the first xylem strand appears in the rachis, all the leaflets are well developed (figure 2D). In Inga, on the other hand, the first part of the primordium to develop is the terminal point, which in the half grown leaf appears like a continuation of the rachis (figure 4A, 4C). This structure develops a xylem strand considerably before any leaflet primordia are visible, and by the time these primordia are clearly evident, the terminal point is almost full grown, with its epidermal cells completely differentiated (figure 4B). The chief feature of the leaf development of Inga, therefore, is the great retardation of the formation of lateral leaflets. The same is true of Ceratonia, only to a lesser degree.

Following Von Baer's principle of embryonic similarity as a modification of the so-called law of recapitulation, we can suggest the following phylogenetic sequence to explain this developmental pattern. The original ancestor of Inga may be presumed to have been mesophytic, with odd-pinnate leaves. Then adaptation to aridity caused reduction of the lateral leaflets and elimination of the terminal one. From the genetic-ontogenetic point of view, this reduction was brought about through mutations retarding the development of the leaflets in relation to the rachis. Then readaptation to mesophytic conditions was brought about through mutations acting late in leaf development, these being more easily established because they caused less disruption of the developmental pattern than would mutations affecting earlier stages. They caused the leaflets to continue growth at the expense of the rachis in later stages of development. It is interesting to note that Inga has several specializations in reproductive structures relative to other Mimosoideae. Its corolla is strongly sympetalous, its filaments are united into a tube, and its mature pod is very large and indehiscent.

Another leaf type in the Leguminosae which appears to have had a complex evolutionary history involving adaptation to xeric and readaptation to mesic conditions is the bipinnate type. The bipinnate leaves of this family, which are predominant in the subfamily Mimosoideae and common in the Caesalpinoideae, are all evenly bipinnate, with vestigial points at the ends of both the main rachis and the rachises of the pinnae (figure 3B). The development of the leaves on adult shoots of *Caesalpinia spinosa* (Molina) Kuntze shows essentially the same features as that of Inga (figure 5, A-E). The terminal points of both the main and the side rachises develop precociously, and the initiation of leaflet primordia is much retarded.

An even more interesting feature is shown in the early development of the seedling of both Caesalpinia and Acacia. In *Caesalpinia spinosa*, the first leaf above the cotyledons is evenly once pinnate, with three pairs of leaflets; the second bears just two entire leaflets; while the third and fourth are bipinnate with a single pair of pinnae (figure 5F, 5G, 6). The

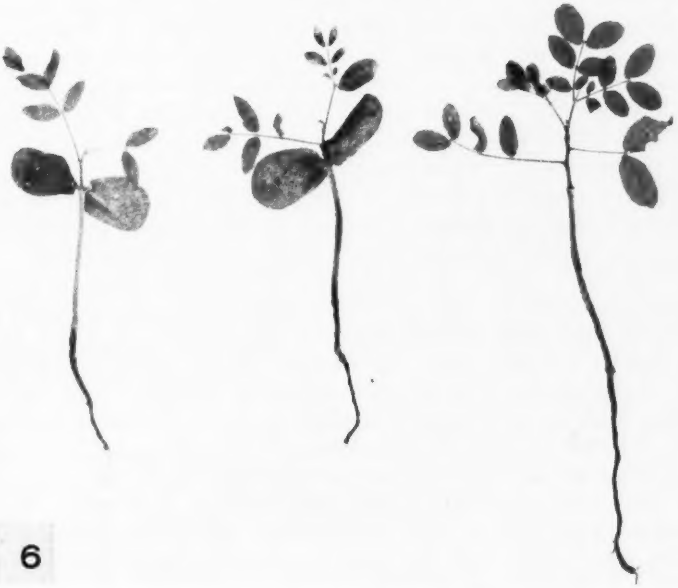

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FIGURE 6. Seedlings of *Caesalpinia spinosa*, showing the morphology of the first few leaves above the cotyledons.

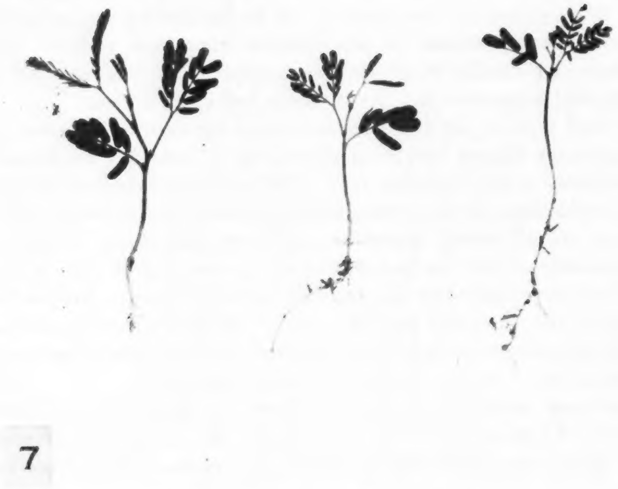

FIGURE 7. Seedlings of *Acacia dealbata.*

three species of Acacia studied (*A. dealbata, A. melanoxylon,* and *A. decurrens*) have similar seedlings, except that the second leaf is already bipinnate (figure 7, 8A, 8B). In both genera the striking fact is that the sequence does not pass directly from the once pinnate type with several pairs of leaflets to the bipinnate type with several pairs of pinnae, as is true in bipinnate leaved genera of other families, such as Koelreuteria (Sapindaceae) and Melia (Meliaceae). There is always an intervening stage of bipinnate leaves with a single pair of pinnae. The development of the second seedling leaf is similar in Caesalpinia and Acacia. The terminal point develops precociously, and the primordia of the leaflets or pinnae are retarded.

This remarkable developmental sequence is explained if we assume that the original ancestors of both Caesalpinia and Acacia once had evenly pinnate leaves. They first evolved xerophytic types whose leaves bore only a single pair of leaflets. Then, the readaptation to mesophytic conditions was accomplished first by mutations changing the leaflets to pinnae bearing secondary leaflets, and second by mutations increasing the number of pinnae. Developmentally, leaflets and pinnae seem to be closely related, as is shown by a seedling of *Caesalpinia spinosa* of which the single pair of divisions on the second leaf consisted of one leaflet and one short pinna. Similar phenomena are recorded by Troll (1939) in Gymnocladus and Gleditschia.

A still more unusual leaf type which may have a similar history is that of the genus Bauhinia, of the subfamily Caesalphinoideae. Most species of this large tropical genus have entire leaves with a peculiar bifid shape

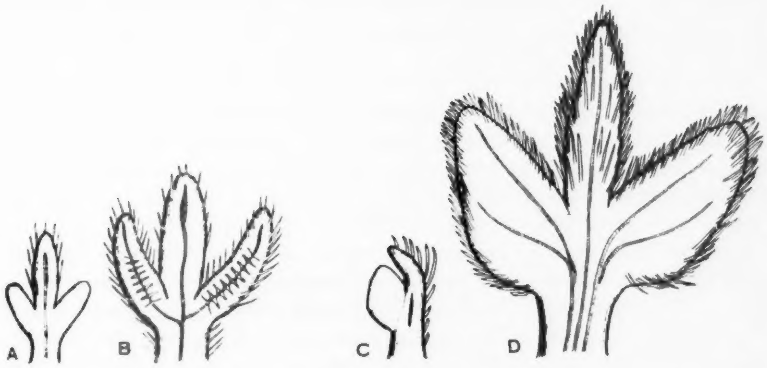

FIGURE 8. Early developmental stages in the seedling leaf of *Acacia dealbata* (A and B) and of the leaf of an adult shoot of *Bauhinia forficata* (C and D). Material for A and B collected in a garden in Berkeley, Calif.; for C and D in Hillside Park, Santa Barbara, Calif. All figures × 33.

(figure 3C). In some species, however, the leaf consists of a single pair of leaflets, with a terminal rachis point, as in the second seedling leaf of *Caesalpinia spinosa.* This fact, together with the presence of this terminal point and the character of leaf venation in all species of Bauhinia indicates that the entire type of leaf has evolved from the type with two leaflets by a process of fusion, as pointed out by Fries (1909). This hypothesis is supported by the course of development of leaves on mature shoots of *B. forficata* and *B. tomentosa.* As in typical even pinnate leaves, the terminal point develops precociously. At an early stage of development, the lobe primordia resemble those of the seedling leaves of Acacia and Caesalpinia, except that they are broader, and bear two vascular bundles rather than one (figure 8C, 8D). Since most of the species of Bauhinia with separate leaflets have relatively small leaves and occur in dry, savanna habitats, while the species with the greatest amount of fusion are large-leaved rain forest types, the fusion process probably accompanied an evolutionary trend of increasing leaf size, associated with adaptation to moister conditions.

Still another leaf type in the Leguminosae which appears to have had a complex evolutionary history is the digitate leaf of Lupinus. In most species of this genus, the leaves on the adult plant have from 7 to 11 leaflets, although in a few species only one leaflet is present. The largest number, 16-17, is found in *L. polyphyllus,* a species inhabiting swamps in the moist region of the Pacific Northwest, hence one of the most strongly mesophytic species of its genus. The seedling leaves in Lupinus always have fewer leaflets than the adult ones. I have observed five in the first seedling leaf of *L. Chamissonis,* three-four in the first leaf of *L. arboreus* and several other species, and only a single leaflet in the first few leaves of *L. Tidestromii,* a species inhabiting beach sands, and strongly xerophytic in the appearance of the adult plant. Since, moreover, the genera related to Lupinus all have leaves with one-three leaflets, there is good reason to believe that the phylogenetic trend in Lupinus has been toward increase in leaflet number, probably associated with adaptation to more mesic habitats.

These examples, picked more or less at random, could probably be duplicated in many other genera of Leguminosae. In addition, evidence for phylogenetic increase in leaf size, associated with adaptation of xerophytes to more mesic habitats, has been found in Rumex (Polygonaceae), Ricinus (Euphorbiaceae), Tibouchina (Melastomaceae), and other genera. It may be a rather widespread phenomenon.

Botanists have been accustomed to thinking of mesophytes as generalized types of plants, and of xerophytes as specialized types derived from mesophytes. This is certainly true in a large number of instances, but the evidence presented above indicates that the trend from xerophytism to mesophytism has taken place several times, even within the limits of a single family. Because of this evidence, and because of the theoretical considerations which might lead one to expect more rapid evolution in arid or semiarid regions, students of plant evolution should not develop preconceived notions about which of these two trends has been the predominant one in the higher plants until the evidence from all disciplines has been obtained and carefully studied.

SUMMARY

Where moisture is a limiting factor, xerophytic plant communities possess fewer species than do the communities of mesophytic regions, but the number of communities per unit of area is likely to be larger than in regions of adequate moisture. This promotes geographic separation of species populations and races, and thus might be expected to speed up evolution. Evidence that certain mesophytic types are derived from xerophytic ancestors is presented for the genera Scorzonera and Tragopogon of the Compositae, tribe Cichorieae, and for certain genera of the subfamilies Mimosoideae and Caesalpinoideae of the family Leguminosae. The evidence in the latter family is derived chiefly from the development of both adult and seedling leaves.

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EXPERIMENTAL MEASUREMENT OF THE RELATIVE VIABILITY OF THE MUTANT EBONY^{11} IN DROSOPHILA MELANOGASTER

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The magnitude of natural selection is dependent upon several variables. It is reasonable to suppose that these variables may be analyzed, by appropriate experimental procedures, into what may be said to comprise the components of selection. Of these several components, the viability of the carriers of a given genotype is one of the more important and easily measured.

In studies of experimental populations of *Drosophila melanogaster* the most evident variable in the external environment is crowding, not only in the population cage itself but also in test samples which are withdrawn from the population and subcultured. As regards its relation to viability, the degree of crowding in a population cage and in subcultures of the population remains unknown unless independent experiments are devised to measure it. The degree of crowding affects viability which in turn affects the adaptive value of the genotype. It is pertinent, therefore, to examine the relations between the degree of crowding and viability.

MATERIAL AND METHODS

Viability can easily be isolated from all other components of selection by using crosses involving a single genetical type of female and a single genetical type of male, *i.e.*, ♀ Aa × ♂ Aa or ♀ Aa × ♂ aa. By varying the degree of crowding for a series of such crosses, the components of viability, as they pertain to the segregating progeny, may be separated as follows. Customarily the selection coefficient s is taken as the complement of the adaptive value (or selective value) W, such that $s + W = 1$ (Wright and Dobzhansky, 1946). Correspondingly we may take a quantity v as the complement of the viability V, letting $v + V = 1$. Since v and V are fractions respectively of s and W, they may be given the same mathematical treatment as the latter. Let

v = the total coefficient (of inviability),
$\dot{v}$ = the component of v independent of the degree of crowding, and
$\hat{v}$ = the component of v dependent upon the degree of crowding.

It can be shown that

$$(1 - v) = (1 - \dot{v})\ (1 - \hat{v}).$$

Hence

$$v = \dot{v} + \hat{v} - \dot{v}\hat{v} \tag{1}$$

and

$$\hat{v} = (v - \dot{v}) \,/\, (1 - \dot{v}). \tag{2}$$

Under conditions where crowding is employed as the variable in the external environment, and where such crowding approaches a minimum, $\hat{v} \rightarrow 0$ and $v \rightarrow \dot{v}$, making it possible to measure v and $\dot{v}$ experimentally and therefore to calculate $\hat{v}$.

In the present experiments $+/e^{11}$ males and females of *Drosophila melanogaster* were crossed; since experiments based on the cross $+/e^{11} \times ee$ have yet to be made, results herein reported pertain only to phenotype. Following a prior fertilization period of four days the heterozygotes were transferred to pint bottle test cultures, each bottle containing 80 ml. of standard medium. In one set of experiments females alone were transferred to the test cultures while in the other set both sexes were transferred (table 1, males indicated in parentheses); each cross was repeated 20 times to give the data of table 1 and all crosses were made at 25° ± 1.5°C.

TABLE 1

RESULTS OF VARIOUS DEGREES OF CROWDING INVOLVING THE CROSS $+/e^{11}$ $+/e^{11}$. EXPLANATION IN TEXT.

Crowding	Observed number of wild	Observed number of ebony^{11}	% ebony^{11}	χ^2	v	$\hat{v}$
1 × (1)	2,282	760	24.98	0.0004	0.0009	0.0
10 × (10)	9,624	3,113	24.44	2.1257	0.0296	0.0287
50 × (50)	15,289	4,519	22.81	50.5	0.1133	0.1125
150 × (150)	11,750	2,355	17.70	518.7	0.3987	0.3982
1 × 1	3,126	1,034	24.86	0.0461	0.0077	0.0068
10 × 10	13,474	4,239	23.93	10.8	0.0562	0.0553
50 × 50	16,591	4,901	22.80	55.3	0.1138	0.1109
150 × 150	12,669	2,279	15.25	758.5	0.4603	0.4599

Experiments were carried out at 25°C., since Kalmus (1945) showed that at or near this temperature the gene ebony is at a selective disadvantage to its wild allele. At other temperatures the behavior of ebony^{11} might of course be expected to give different results; this has been shown by Kalmus (1945) for the mutant ebony in *Drosophila melanogaster* and by Dobzhansky (1947) and Wright and Dobzhansky (1946) for different gene arrangements in *Drosophila pseudoobscura*.

RESULTS AND DISCUSSION

The results of the experiments are given in table 1. The first column gives the degree of crowding according to the numbers of parents per culture. χ^2 is calculated for an expected 3 : 1 ratio. The quantity v in column six of table 1 is calculated directly from the experimental data by the formula

$$v = (D - 3R)/D,$$

where D = the observed number of wild-type flies and R = the observed number of ebony^{11} flies. The quantity $\hat{v}$ in the seventh column is calculated from (2).

It will be noted that the deviation from a 3:1 ratio for crosses 1 × (1) and 1 × 1 is not significant for the sample sizes obtained. Here $\dot{v} \to 0$, but it may not necessarily be 0, as would possibly be shown by a larger sample size. If X^2 values for these crosses are taken to indicate a lack of significance, then the differences between v and $\hat{v}$ are not significant either, and $\dot{v} = 0$. But since a viability difference between wild and ebony^{11} appears as crowding increases, the difference between wild and ebony^{11} is ostensibly real and the differences between v and $\hat{v}$ are real though small. It is interesting to note that from (1)

$$dv = (1 - \dot{v})\ d\hat{v}.$$

Hence as $\dot{v} \to 0$, v and $\hat{v}$ tend to change at the same rate and to be identical at $\dot{v} = 0$.

As regards the particular strain of the mutant under consideration, e^{11}, it can be seen that at minimal crowding the viability (V) is nearly equal to unity, compared with that of wild type. From this it might be thought that the viability of the two alleles, and therefore their adaptive values, would be the same. But since viability is but one of the components of the adaptive value, and since under conditions of maximal crowding viability is reduced to 54 per cent of that of wild type, such a conclusion would obviously be unwarranted.

Under the stated conditions of the experiments it can be seen that the relative viability of the homozygous carriers of e^{11} varies according to the degree of crowding, ranging from very nearly 100 per cent to 54 per cent as the degree of crowding increases. As concerns genes having genetical properties similar to those of e^{11}, it is evident that the quantitative effects of crowding variations must be known before their behavior in populations and subcultures can satisfactorily be interpreted. In general, it seems desirable to determine the effects of such variations wherever gene frequencies have to be measured by indirect means, as they do, for example, in the case of genes which are completely recessive.

SUMMARY

In experimental populations of *Drosophila melanogaster* involving the mutant ebony^{11}, the magnitude of natural selection is influenced by crowding variations. A method is described by which one of the components of selection, inviability, may be isolated, analyzed and measured in relation to different conditions of crowding. Inviability is divided into two components, one dependent upon and another independent of the degree of crowding. Experiments are designed to show the differential effects of crowding upon inviability and its components and upon their complements. The experimental data indicate that as crowding approaches a minimum the wild-type and mutant flies become very nearly equal in viability, while as the degree of crowding increases, the viability of the mutants is considerably decreased. The quantitative relations between viability and a given degree of crowding have been determined for the homozygous carriers of ebony^{11}

and can be taken as standards to aid in the interpretation of the effects of selection on experimental populations and on subculture tests of these.

ACKNOWLEDGEMENTS

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STUDIES ON CHEMICAL MUTAGENESIS UTILIZING NUCLEIC ACID COMPONENTS, URETHANE, AND HYDROGEN PEROXIDE[1]

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INTRODUCTION

Since the striking proof by Auerbach and Robson (1946) of the mutability of mustard gas when applied to Drosophila, numerous other chemical substances have been tested using different methods of treatment. The alleged specific mutagenic effects of feeding nucleic acids (Gershenson, 1939, 1940, 1948, and Tarnavsky, 1938, 1939) have not been substantiated by other investigators (Rapoport, 1940; Muller, 1941). Nevertheless, the high concentration and supposed important role of desoxyribonucleic acid in chromosomal material suggests the possibility that modifications in quantity or quality of the natural components of nucleic acid might induce mutations, possibly of a specific type. Perhaps by supplying excessive amounts or by prematurely providing the germ cells with these chemicals alterations in the gene could be produced. This paper reports the results of experiments designed to determine whether or not certain nucleic acid components and other nitrogen bases (adenine, guanine, cytosine, thymine, uracil, thiouracil and xanthine can induce sex-linked lethal mutations in *Drosophila melanogaster*.

Also reported are results of experiments testing the effectiveness of urethane and hydrogen peroxide separately and in combination in producing sex-linked lethals. Hydrogen peroxide was found by Wyss *et al.* (1947) to have an indirect effect when treating the substrate of *Staphylococcus aureus*. Vogt (1948, 1950) found that injecting sublethal doses of ethylurethane into adult males of Drosophila increased the mutation rate significantly.

METHODS

Only males of the Oregon-R stock of *Drosophila melanogaster* were used throughout. All flies were raised at 21°C. on standard cornmeal-agar medium. In all larval experiments third instar larvae were used.

In the majority of the present experiments, the substances used were injected into the larvae in order that the solution could be placed in direct contact with or even within the testis. The application of the micro-injection technique has two advantages: it permits the investigator to maintain control of the exact quantity of substance available to the organisms, and at the same time reduces the likelihood that intermediate products will be produced when the chemical is mixed with the food or reacts in the digestive tract.

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[1] This paper comprises part of a thesis submitted in partial fulfillment for the degree of Doctor of Philosophy.

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An injection apparatus was made by mounting a 1 cc. B-D Yale tuberculin syringe on a ring stand base and by fitting the plunger with a spring and screw device. The screw was mounted in such a way that each revolution of the screw compressed the spring and sent the plunger deeper into the barrel. A hypodermic needle (26 gauge) served as a coupler between the syringe and the 0.9 mm. nylon tubing, into whose free end was placed a minute, glass micropipette. All connections were sealed with sealing wax or bees' wax. The apparatus was calibrated in such a way that, after accounting for loss of solution during the operation, approximately 1/100 ml. was injected into each larva.

The male larva to be injected was placed on a piece of filter paper and inactivated by rolling it on its long axis with another piece of filter paper, and then was held on its side with forceps. An attempt was made to thrust the pipette into the testis, thus applying the solution directly to the germ cells. To increase the chances of striking a testis, the thymine injection series was done on both sides of the larvae. After injection the larvae were placed in food vials which contained wet cellucotton. Larvae which were visibly damaged or overly inflated were discarded immediately.

Holtfreter's saline, pH 7.85, was used as a control in the injection series and as a solvent for the nitrogen bases and for urethane. All injections of nitrogen bases were made with a 10^{-4} molar concentration. The concentrations used permitted approximately 10 per cent of the larvae injected to survive.

In the 3 per cent H_2O_2 series a metal free system was used by attaching the nylon tubing directly to the nose of the syringe. The apparatus was cleaned by using first double distilled water and then rewashing with 3 per cent H_2O_2. The saline solution was omitted from the peroxide solution in order to avoid as far as possible the decomposition of the peroxide.

An M/4 concentration of urethane in Holtfreter's saline was injected into the ventral surface of the abdomen of etherized, adult, 48 hour-old, unmated males. A group of these injected adults was placed in a creamer containing food which was kept for 24 hours in a darkened desiccator containing 15 cc. of superoxol.

The effect of superoxol fumes alone was tested on third instar, male larvae (6 and 12 hour periods) and on 24 hour-old unmated male imagos (24 hour treatment periods). The larvae were treated while in a stender dish, the bottom of which was covered with wet filter paper; the adults were in small creamers with food.

An effort was made also to combine the action of peroxide fumes with thymine injections to determine whether an additive or synergistic effect might result from their combination. All peroxide fume experiments were done in the apparatus above.

Since the results of a suspected mutagen become more trustworthy when tested simultaneously with the controls, the injections of Holtfreter's salt solution into larvae were done concurrently with those of the nitrogen bases; also urethane injections were done at the same time as the combination treatment with urethane and superoxol fumes.

After these varied types of treatment, the flies were all tested for X-chromosome lethals with the Muller-5 technique. Each adult male was mated to three virgin, Muller-5 females and the resulting heterozygous F_1 females were placed individually into food vials with three Muller-5 males. The F_2 cultures were examined under the dissecting microscope *en masse* while in the vial. The lethal cultures were recognized easily by the absence of the wild type males in the F_2 cultures; all cultures which were suspected of containing lethals or semi-lethals were anaesthetized and examined carefully and were continued through the F_3 generation before the conclusion was drawn that no lethal was present in the treated X-chromosome.

In the cases in which several lethals were obtained from a single male, it was necessary to determine if they had a common origin or if they had originated independently. This was done by means of the following cross-over tests: males from a *y Hw w m f* stock were mated to virgin heterozygous females containing the lethal; F_1 females showing *Hairy-wing* were backcrossed to their brothers and only the males were counted in the F_2. The location of these lethals was necessary for the scoring of mutations. If several lethals from one male are distributed along the X-chromosome, the assumption can be made that they are different mutations which must be scored as individual events; on the other hand, if they all have the same locus, it may be assumed that they have a common origin and must be scored as one lethal.

OBSERVATIONS AND RESULTS OF EXPERIMENTS

Larval Injections

As a control, 40 male larvae were injected with Holtfreter's saline. All 15 males which survived to adulthood appeared to be normal wild type and fertile. The technique employed produced no mutations when Holtfreter's saline was injected alone.

In the experiments using the nucleic acid purines, adenine and guanines, abnormalities were found. The use of a naturally occurring purine base, xanthine, produced no visible abnormalities. The pyrimidine bases of desoxyribonucleic acid, thymine and cytosine, failed to increase the lethal mutation rate. Thymine, as previously stated, was injected on both the right and left side of the larvae. One of the surviving adults was a sterile bilateral gynandromorph. Injections with cytosine produced a higher mortality rate than the other components of desoxyribonucleic acid used. Only 7 males from the 155 injected reached the adult stage; however, these proved to be unusually fecund. Uracil, a normal component of ribonucleic acid, produced one sterile adult which had a very curved abdomen. The adults which emerged from the larval series injected with thiouracil, the sulphydril analogue of uracil, were all normal and fertile. A summary of the results of the preceding experiments—the control, the purines, and the pyrimidines—are collected in table 1.

TABLE 1

COLLECTED RESULTS OF CONTROLS AND NITROGEN BASES

Experiment	Number injected	Survived	% Survived	Sterile	Fertile	% Fertile	X-chromosomes tested	Range* within experiment	Lethals	% Lethals
Control	40	15	37.6	0	15	100.0	742	18–77	0	0.0
Adenine	250	26	10.4	2	24	87.5	1210	7–60	1	0.0092
Guanine	110	14	12.7	2	12	85.6	600	17–84	0	0.0
Xanthine	101	12	11.9	0	12	100.0	716	29–77	2	0.27
Uracil	187	13	6.9	1	12	92.4	613	39–56	0	0.0
Thymine	234	11	8.9	1	10	91.0	475	27–54	0	0.0
Cytosine	155	7	6.9	0	7	100.0	352	32–57	0	0.0
Thiouracil	113	9	9.6	0	9	100.0	504	51–61	0	0.0
Totals	1190	107	9.0	6	101	94.5	6212		3	0.05

* Represents the extremes found in each experiment.

Thymine injections of larvae were tried in combination with superoxol fumes. This treatment was repeated seven times (using 10 larvae at a time) with the same results: no larva survived the treatment.

Injection of 3 per cent H_2O_2 produced a much higher mortality rate than the other treatments. From 130 males injected only five adults were recovered (all apparently normal). No lethals were found in this series.

Hydrogen Peroxide Fumes on Larvae

Since hydrogen peroxide is thought to be partially responsible for chromosomal aberrations in radiation work (Lea, 1947) and to have an indirect effect when the substrate of *S. aureus* is treated (Wyss *et al.*, 1947), it was tested for mutagenic ability. In the 6-hour treatment 283 chromosomes were tested and in the 12-hour treatment 672 chromosomes. No lethals were revealed in either case.

TABLE 2

ADULTS INJECTED WITH M/4 URETHANE AND COMBINED WITH SUPEROXOL FUMES

Male	Chromosomes	Lethals	Male	Chromosomes	Lethals	Male	Chromosomes	Lethals
a	47	1	i	52	3	q	55	0
b	57	1	j	53	1	r	553	1
c	52	0	k	60	0	s	55	0
d	56	0	l	55	0	t	31	0
e	60	2	m	54	0	u	76	1
f	50	0	n	20	0	v	57	0
g	53	3	o	51	2	w	41	0
h	56	0	p	59	2			

Treatment of Adults

Thirteen adult male Drosophila were exposed to superoxol fumes. Surviving, after 24 hours, were 11 flies from which 549 X-chromosomes were tested for lethal mutations. No mutations were found.

As a control for this experiment, 45 adult males were injected with M/4 urethane (ethyl carbamate). After 24 hours these were examined and it was apparent that only 12 could be mated. The chromosomes per male ranged from 39 to 69 and totaled 641. Two sex-linked lethals were found in this urethane series.

The combination treatment using injections of M/4 urethane with superoxol fumes applied for 24 hours was begun with 55 males; however, only 23 of these gave rise to progeny. From a total of 1,203 chromosomes examined, 17 lethals were found (see table 2). The loci of the multi-lethals were determined and it was deduced that at least 11 of the 12 multi-lethals arose independently.

The duration of the larval instar and time of pupation were manifestly lengthened with the injections of the nucleic acid components when compared with all other series of injections.

DISCUSSION

Although the use of normal nucleic acid or its components has failed to produce significant numbers of mutations except in bacteria there is no doubt that some of these substances may modify growth and development of Drosophila (adenine sulfate, Wilson, 1942; guanine, Wilson, 1943a; uracil, Wilson, 1943b; thymine, Wilson, 1944). The fact that substances of this type can be mutagenic has been shown by using simpler organisms, such as bacteria in which there is a closer contact of the genes with the mutagenic agent. The inclusion of p-xanthine and adenine by Novick and Szilard (1951) as mutagenic agents makes it obvious that the problem of cellular permeability is not such an obstacle in bacterial genetics as in Drosophila studies.

Purines and pyrimidines, when injected by the method used in these experiments, failed to increase the X-chromosome lethal mutation rate in *Drosophila melanogaster*. Although an attempt was made to strike the testis itself and thus bathe it with the solution being tested, there was no way of knowing that the test substances actually reached the genes or that they were not altered before reacting with the genes.

In the control series injected with Holtfreter's saline, about 38 per cent of the larvae survived to adulthood, while the average of the other larval injection series was about 8 per cent. The difference of 30 per cent between the control and experimentals is indicative that the nitrogen bases did interfere with some physiological process or processes of Drosophila.

All experiments involving the direct action of H_2O_2 were negative. Exposing larvae and adults to superoxol fumes or injecting larvae with 3 per cent H_2O_2 produced no mutations. It is suggested that the detoxification mechanism of the organism in both stages of the life cycle was able to decompose the peroxide when presented in a vapor externally or as a weak solution internally. The combination of an injected pyrimidine base, thymine, with superoxol fumes did not permit any larvae to survive. Perhaps this was due to killing of the larval tissue, particularly at the point of injury by the strong fumes.

The sex-linked lethal mutation rates in the various urethane series were compared to each other and to the spontaneous rate of the Oregon-R stock in this laboratory (Sturtevant, 1951). Comparison of the urethane injected series (0.31 ± 0.22%) to the untreated males indicated that the mutation rate was not increased significantly. On the other hand, the results of the series in which urethane and superoxol were combined (16/1203 or 1.33 ± 0.33%) compared with those of the untreated males (5/1949 or 0.26 ± 0.12%), or to those of the first urethane series (2/641 or 0.31 ± 0.22%) showed that the X-chromosome mutation rate was significantly increased. Since it is not likely that oxygen from the peroxide oxidized urethane, it is suggested that the increased oxygen tension increased the metabolic rate within limits, and was responsible for making the germ cells receptive to the mutagenic action of urethane. Therefore, the action of urethane plus superoxol fumes is considered to be synergistic in producing sex-linked lethal mutations.

A study of the distribution of the multi-lethal mutations from individual males of the last series reaffirms Vogt's (1950) conclusion that it is not likely that urethane has a specific action on certain loci.

Although Vogt (1948, 1950) obtained a higher mutation rate with urethane alone or when combined with a temperature shock, it should be noted that a different salt (sodium chloride or potassium chloride) was used as a solvent for the urethane and that a different type of wild stock was used in her experiments. It is quite possible that Holtfreter's saline served as a good buffer or protective mechanism inhibiting the chemical mutagen from reaching the nucleus. The use of different experimental stocks *a priori* supposes different modifiers, some of which might offer better protection for the organism against urethane. Thus, it is not surprising that the results obtained differ from those of Vogt.

SUMMARY

1. Injection of 10^{-4} molar solutions of normal nucleic acid nitrogen bases (adenine, guanine, uracil, thymine, and cytosine) in Holtfreter's saline into the area of the larval testis failed in all cases to increase the sex-linked lethal mutation rate.

2. The use of a naturally occurring purine, xanthine, in a 10^{-4} concentration also failed to increase the lethal mutation rate.

3. Thiouracil (10^{-4} molar concentration in Holtfreter's saline), a sulphydril analogue of the pyrimidine, uracil, did not increase the mutation rate when injected into male larvae.

4. The direct action of superoxol fumes on male larvae and adults gave negative results. This was true also for the larval series injected with 3 per cent hydrogen peroxide.

5. Treating the adults by injecting with urethane in Holtfreter's saline did not increase significantly the number of lethals; however, combining urethane injections and treatment with superoxol fumes did raise the sex-linked lethal mutation rate significantly. This positive result is deemed to be a synergistic effect.

ACKNOWLEDGEMENT

The author is indebted to Dr. George H. Mickey for his valuable assistance and advice during the course of this work.

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THE AMERICAN SOCIETY OF NATURALISTS

SECRETARY'S REPORT, 1951

The annual business meeting of the Society took place on September 12, 1951, in the auditorium of the Minnesota Museum of Natural History in Minneapolis, following the excellent and well-attended symposium arranged by the Society's Vice-President, B. P. Kaufmann, who presided. The Symposium was cosponsored by the Genetics Society of America. The papers presented at the Symposium will appear in *The American Naturalist* which will also publish the address entitled "Evolution under Domestication," given by President Paul C. Mangelsdorf, on the evening of September 11, 1951.

Patterns of Cellular Organization

"Stereoscopic Studies of Cells and Viruses in the Electron Microscope", by Thomas F. Anderson, Univ. of Pennsylvania, Philadelphia

"The Submicroscopic Structure of Tissue Cells", by Keith R. Porter, Rockefeller Institute for Medical Research, New York

"Molecular Organization in the Cell Nucleus", by Daniel Mazia, University of California, Berkeley, California

"The Pattern of Differentiation in Amoeboid Slime Molds", by John T. Bonner, Princeton University, Princeton, N. J.

During the past year the work of the Secretary has been concentrated on the matter of memberships in the Society. It is gratifying to report that the anticipated drop because of resignations (following the increase in dues attendant upon the assumption by the Society of the editorial direction of *The American Naturalist*) has not materialized to anything like the extent expected. Last year in September the Secretary reported 446 active members, 136 emeritus members, 10 honorary members, making a total of 592. At the meeting in September, 1950, 39 new members were elected, of which 35 accepted membership. The number of emeritus members has increased during the past year by 20. Losses in membership amount in all to 44 (6 deaths reported, 33 resignations, and 5 suspensions for non-payment of dues). The loyalty of the membership is shown by the fact that the resignations and suspensions have amounted to no more than 8.5 per cent of the active membership. At the Minneapolis meeting 61 new members were elected, and by November 6, 1951, 39 had accepted. There are thus at the present time, according to the Secretary's records, 463 active members, 156 emeritus members, and 10 honorary members, a total of 629. However, the number of emeritus and honorary members has now increased to 26.5 per cent of the total membership. There thus continues to be a need for the election of active younger members.

The Secretary is pleased to report that his efforts to secure the nominations to membership of well-qualified biologists has met with fine cooperation from not a few members, although a greater distribution of effort in this direction is still to be desired.

At the annual meeting a number of important steps were taken. Interim reports from the Secretary, the Treasurer, and the Editor of *The American Naturalist* (see below) were read and approved. Copies may be obtained from the secretary upon application by members of the Society.

It was voted, upon recommendation of the Executive Committee, that the Society should become a member society of the American Institute of Biological Sciences, beginning January 1, 1952. Our Society was among those instrumental in founding the AIBS, it has profited from the work of the AIBS in arranging the last two annual meetings (at Columbus and Minneapolis), and it had previously instructed the Executive Committee to join the AIBS whenever the finances of the Society might permit. The favorable report of our Treasurer, and the fact that most, if not all, of our members belong to other societies already members of AIBS, has made the time seem ripe. The annual dues to AIBS will approximate $250.00, and our favorable balance will make it possible to meet this annual charge for a number of years even if other expenses were completely to consume our income. It is expected, however, that use of the mailing and office services of AIBS will effect some savings in the present expenses of the Society's Secretary and Treasurer. It was also felt that it was unfair for the Society to continue to profit from the services of the AIBS in arranging annual meetings without bearing our due part of the expense. If the Society continues to meet annually with the AIBS, as at present planned, membership in the AIBS would seem to be a real obligation.

It was voted to hold the next Annual Meeting with the AIBS at Cornell University in Ithaca, New York, in September, 1952.

It was voted to give each of the ten Honorary Members of the Society a subscription to *The American Naturalist* for the year 1952.

There was considerable discussion of the desirability of having two annual symposia sponsored by the Society, one at the Annual Meeting held with the AIBS, the other at the AAAS meetings in December. It was generally agreed that this would add materially to the success of the Society in helping to unify and integrate the several fields of biology, both by covering more areas of our science and by reaching not only those biologists and biological societies meeting in one region with the AIBS but also those meeting in another with the AAAS. It was also pointed out that such a measure would increase the supply of the kind of manuscripts most desired for publication in *The American Naturalist*. However, there was some fear that the arrangement of two symposia within the space of a few months would overburden the Vice-President, upon whom this task falls. No formal action was taken, but the question is to be considered further. A solution may be proposed which would avoid overburdening our own officers and yet meet the need. It should be possible, namely, for the Society to arrange the symposium at the AIBS meeting (cosponsored as at present by other societies, as by the Genetics Society this September), and in addition to cosponsor a symposium, arranged chiefly by other societies or sections but consonant with our aims, at the AAAS meetings.

The Nominating Committee (Marcus Rhoades, Chairman) presented the names of Sewall Wright, Ernest D. Burton Distinguished Service Professor of Zoology at the University of Chicago, and Professor C. B. Van Niel, of the Hopkins Marine Station, Stanford University, for President and Vice-President of the Society, respectively. No other nominations being made, they were unanimously elected to these offices for the year 1952.

Th. Dobzhansky, Marston Bates and Carl Hubbs were appointed to the Editorial Board of *The American Naturalist.*

A resolution of warm appreciation was passed by unanimous vote to thank Dr. Sheldon Reed, of the University of Minnesota, for his untiring work as our local representative in arranging the Annual Meeting; to thank our host institution, the University of Minnesota, for its generous hospitality; and to thank Dr. Clarence Hylander and the other staff members of the AIBS, for their most efficient organization of a pleasant and profitable meeting.

Respectfully submitted,
BENTLEY GLASS,
Secretary

November 6, 1951

NEW MEMBERS, 1950

Mary L. Austin, Wellesley College.
Daniel I. Axelrod, University of California at Los Angeles.
David M. Bonner, Yale University.
Werner Braun, Chemical Corps, Camp Detrick.
Samuel Brody, University of Missouri.
John B. Calhoun, Army Medical Center.
Hampton L. Carson, Washington University.
Raymond B. Cowles, University of California at Los Angeles.
Edward S. Deevey, Yale University.
Paul L. Errington, Iowa State College.
John L. Fuller, Roscoe B. Jackson Memorial Laboratory.
Melvin M. Green, University of California.
Felix Haurowitz, Indiana University.
Norman H. Horowitz, California Institute of Technology.
William Hovanitz, University of San Francisco.
G. Evelyn Hutchinson, Yale University.
A. I. Lansing, Washington University School of Medicine.
John R. Laughnan, University of Illinois.
Joshua Lederberg, University of Wisconsin.
Edward B. Lewis, California Institute of Technology.
Herschel K. Mitchell, California Institute of Technology.
Gairdner B. Moment, Goucher College.
John A. Moore, Columbia University.
Joseph G. O'Mara, Iowa State College.
Jane Oppenheimer, Bryn Mawr College
John R. Preer, University of Pennsylvania.

Hans Ris, University of Wisconsin.
W. L. Russell, Oak Ridge National Laboratory.
E. R. Sears, University of Missouri.
G. F. Sprague, Iowa State College.
Adrian M. Srb, Cornell University.
Harrison D. Stalker, Washington University.
S. G. Stephens, North Carolina State College.
Oswald Tippo, University of Illinois.
R. P. Wagner, University of Texas.

NEW MEMBERS, 1951

Thomas F. Anderson, University of Pennsylvania.
Marston Bates, The Rockefeller Foundation.
David W. Bishop, California Institute of Technology.
John Tyler Bonner, Princeton University.
Meta Suche Brown, Agricultural and Mechanical College of Texas.
Arnold M. Clark, University of Delaware.
Ralph E. Comstock, North Carolina State College.
Lincoln Constance, University of California.
Bernard D. Davis, Tuberculosis Research Laboratory.
Everett R. Dempster, University of California.
Vincent G. Dethier, The Johns Hopkins University.
Graham DuShane, Stanford University.
Frank H. J. Figge, University of Maryland School of Medicine.
Walter S. Flory, Jr., University of Virginia.
Benson E. Ginsburg, University of Chicago.
Arnold B. Grobman, University of Florida.
Howard L. Hamilton, Iowa State College.
J. George Harrar, The Rockefeller Foundation.
Gertrude Heidenthal, Union College.
Fred H. Hull, University of Florida.
Theodor Just, Chicago Natural History Museum.
Benjamin J. Kaston, Teachers College of Connecticut.
I. Michael Lerner, University of California.
M. W. Parker, United States Department of Agriculture.
Grace E. Pickford, Yale University.
Frank A. Pitelka, University of California.
Dorothy Price, University of Chicago.
John R. Raper, University of Chicago.
Robert G. Reeves, Agricultural and Mechanical College of Texas.
Charles M. Rick, University of California.
Benjamin P. Sonnenblick, Rutgers University.
Arnold H. Sparrow, Brookhaven National Laboratory.
Karl A. Stiles, Michigan State College.
Gordon L. Walls, University of California.
Talbot H. Waterman, Yale University.
W. Gordon Whaley, University of Texas.
Thomas W. Whitaker, United States Department of Agriculture.
Maurice Whittinghill, University of North Carolina.
Carroll M. Williams, Harvard University.

DEATHS REPORTED SINCE LAST REPORT

John T. Buchholtz
L. L. Burlingame (1950)
Otto C. Glaser
Jesse M. Greenman
Charles G. Rogers
Morris Steggerda
J. P. Visscher

Vol. LXXXVI, No. 826 The American Naturalist January-February, 1952

BOOK REVIEWS

TWO RECENT VERSIONS OF EUGENICS

THEODOSIUS DOBZHANSKY

Changes in the intellectual climate in the United States after the close of the war have brought, among other things, a resurgence of interest in eugenics and in population problems. A revised edition of "Preface to Eugenics"[1] by Frederick Osborn, the president of the American Eugenics Society, and the popularly written "Human Fertility: The Modern Dilemma"[2] by R. C. Cook, are authoritative accounts which reflect somewhat different schools of thought in modern eugenics.

Since eugenics is supposedly concerned with applications of the basic findings of genetics to human problems, geneticists felt understandably disturbed by the very unfortunate uses to which eugenics was sometimes put by political propagandists. It is, accordingly, most gratifying to have Osborn emphasize that the "belief in the influence of heredity overreached itself when it was used—as it still is all too often—to justify the continued domination of some particular caste or group," and that "Recently it has come to be recognized that eugenics is not in opposition to efforts to improve the environment, but in many cases a necessary supplement to their success. As this realization spreads, people will find it easier to consider problems of individual differences in less emotional, more rational, terms." Unfortunately, one looks in vain for an equally clear statement in Mr. Cook's book.

Osborn's summary of the present state of the nature-nurture problem is fair and convincing. Beyond reasonable doubt, the variance in intelligence and in personality traits observed among members of human isolates has both genotypic and environmental components. But, "there is at present no scientific evidence to justify imputing differences in intellectual capacity to race," and "In the present state of knowledge, the argument that races differ biologically (in intellectual capacities) is more likely to be used to satisfy an emotional bias than because there is evidence to give it validity." What a far cry from the pseudo-science that has so often utilized the name of eugenics!

The rapid growth of human populations, and chiefly in countries which are crowded already far beyond optimal population density, is discussed briefly by Osborn, at length and with great passion by Cook. To Cook, the uncontrolled fertility is "the most ominous force in the world today"—just "next to the atom bomb," and it brings with it "the modern dilemma."

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[1] "Preface to Eugenics," by Frederick Osborn. 333 p. $4.00. Harper and Brothers, New York, 1951 (revised edition).

[2] "Human Fertility: The Modern Dilemma," by R. C. Cook. 380 p. $4.50. William Sloan, New York, 1951.

One must certainly agree with Osborn that the problems of overpopulation "are both very grave and very complex, and until we know how they are being solved, no eugenic prognosis is possible." But to Cook the overpopulation is the main axis of eugenics. For people not only reproduce too much, but it is chiefly the wrong people who do the reproducing. Families with more education have fewer children than those with less education, the more well-to-do are less fertile than those with lower incomes, and, of course, the East breeds more rapidly than the West. Now, the less fertile groups have higher I.Q.'s than the more fertile ones. Hence, the I.Q. in the United States and in Western Europe is bound to decline, although Cook is not sure whether the decline will amount to 1 per cent or as much as 4 points per generation.

The fact that the future generations are being brought up by parents who by their economic and educational status are least well qualified to raise them is clearly undesirable. But it is going beyond the evidence to preach the inevitability of a biological doom on this basis. Osborn puts the matter succinctly in these words:

"In the light of recent studies which are more scientific than any available in the past, social class differentials in births do not appear so disturbing from the eugenic point of view, though they may seriously retard cultural advance. The present author fails to view their eugenic aspects with alarm...." The problem is surely not thereby solved, but it is at least placed in its proper perspective.

Osborn's book has so much to recommend it that it is a pity to have to temper the praise with some criticism. Scientific eugenics can be based only on findings of population genetics. A "Preface to Eugenics" should, then, acquaint the reader with the principles of population genetics beyond a rather perfunctory discussion of Hardy's equilibrium. The potentialities, as well as the difficulties, of eugenic programs aiming to reduce or eradicate hereditary diseases can not be understood without knowing the effects of different forms of selection and of mutation on gene frequencies. Even though these matters require introducing some "mathematics," which may frighten some readers, the avoidance of the subject leaves the reader unfamiliar with the essentials. Nor is it good to state without fuller explanation that "Except for the rare occasion of mutation, however, the genes are passed on from one generation to another unchanged and without being affected by any changes which may have taken place in the body or mind of their temporary custodian." Statements of this sort lend color to the assertions of Lysenkoists that genetics considers genes unchangeable. And the conclusion that "Children tend to be like their parents in hereditary capacity for intelligence" means no more than that the heredity is inherited.

PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

EDITORIAL OFFICE
The American Naturalist
635 W. 247 St.
New York 71, N. Y.

Allee, W. C., 1951. Cooperation among animals. 233 p. $3.50. Henry Schuman, New York.

This is a revised edition of an important book by one of the foremost living ecologists. Its main thesis is that all, or almost all, organisms are more or less interdependent. Accordingly, cooperation is as widespread and important in evolution as competition and struggle. The presentation is remarkably simple and lucid, making the book readable to biological laymen.

T.D.

Clausen, Jens, 1951. Stages in the evolution of plant species. 206 p., ill. $3.75. The Macmillan Company, New York.

This compact but elegantly published volume gives in a direct, charmingly simple, and in places almost conversational language, a summary of the very significant work of J. Clausen and of his colleagues, D. D. Keck and W. M. Hiesey, on the experimental taxonomy of plants. A part of this work has previously been published in a series of monographs, but much of it is quite new. Especially important are new data on the systematic, ecologic, and cytogenetic relationships between races and species of tarweeds (Compositae, Madiinae). The interpretative sections of the book are brief; they show influences of concepts advanced by the Swedish botanist, Turesson, tempered by the robust scepticism of the author. The book abounds in excellent illustrations, some of which will doubtless grace the pages of textbooks and manuals for years to come.

T.D.

McDougall, W. B., and Omer E. Sperry, 1951. Plants of Big Bend National Park. 209 p., ill. $1.00. U. S. Government Printing Office, Washington, D. C.

Martin, Gustav J., 1951. Biological Antagonism—The theory of biological relativity. 516 pp. $8.50. The Blakiston Co., Philadelphia.

Dr. Martin's book is directed primarily at the biochemist and pharmacologist. It has, however, interest for other biologists as it deals with the fundamental problem of specificity. Its organization is largely collative, and most attention is devoted to the action of metabolite analogues of the vitamins, amino acids and other biologically important substances. The approach is in terms of structural displacement which forms the basis of the modern rational approach to chemotherapy. The theory of biological relativity states that no single molecular structure possesses a function not shared in some degree by structurally related molecules. It is proposed that antagonistic phenomena are the buffering mechanisms essential to the constancy and orderliness of living processes. This theory has been elaborated on different evidences by Davis (Experientia 6:41-50, 1950) but the latter's work is not referred to. Other problems with which the author grapples have been illuminated by published work to which he also does not refer. The theoretical problems involved in biological antagonism are not treated in a way as profound or analytical as that of the Works in their *The Basis of Chemotherapy* (Interscience, 1948). But it would be a dull biologist who could read far in Dr. Martin's book and not find his imagination stimulated.

F.J.R.

Tattersall, Walter M., 1951. A Review of the Mysidacea of the United States National Museum. 292 p., ill. $1.00. Bulletin 201, Smithsonian Institution, Washington, D. C.

West, Edward S., and Wilbert R. Todd, 1951. Textbook of Biochemistry. 1345 p., ill. $12.00. The Macmillan Company, New York.

ERRATA

In the article "Metabolic Types and Growth Types" in THE AMERICAN NATURALIST, Vol. LXXXV, March-April, 1951, by Ludwig von Bertalanffy, the formula for weight growth (p. 113, Fig. 1) reads:

$$y = \left[\sqrt[3]{Y} - \left(\sqrt[3]{Y} - \sqrt[3]{y_0}\right) e^{-kt}\right]^3 .$$

On p. 115, line 9 from bottom, read: "so that the exponent *n* (instead of *m*) can be set equal to 1."